Species distribution modelling of stream macroinvertebrates at the catchment scale

---

Inaugural-Dissertation

zur

Erlangung des Doktorgrades

Dr. rer. nat.

der Fakultät für Biologie

an der

Universität Duisburg-Essen

vorgelegt von

Maria Gies

geboren in Frechen

Februar 2015

Die der Arbeit zugrunde liegenden Datenerhebungen wurden an der Abteilung für Aquatische Ökologie der Universität Duisburg-Essen durchgeführt.

1. Gutachter: Prof. Dr. Daniel Hering

2. Gutachter: Prof. Dr. Ellen Kiel

Vorsitzender des Prüfungsausschusses: Prof. Dr. Jens Boenigk

Tag der mündlichen Prüfung: 08. Juni 2015

Acknowledgements

First of all I wish to thank my supervisor Prof. Dr. Daniel Hering for giving me the opportunity to do research on the complex topic of this thesis including intensive and fulfilling field work, for improving the structure and content of this thesis and for his guidance around the obstacles of a PhD project. Further, I am grateful to Dr. Christian K. Feld for stimulating fruitful discussions and constructive comments on the methods and text and for his support in publishing two chapters of this thesis. I greatly acknowledge the close collaboration with Martin Sondermann, for sharing data, his support and ideas and lots of discussions.

This thesis was financially and ideally supported by the Deutsche Bundesstiftung Umwelt (DBU) which provided support and funding for three years. I am also grateful to the North Rhine-Westphalia State Agency for Nature, Environment and Consumer Protection (LANUV) for providing the digital river network (3A) and macroinvertebrate and physical habitat quality data. I also thank the district government Cologne in North Rhine-Westphalia (Geobasis NRW) for providing the digital terrain model (DGM5).

For the dedicated assistance in the field work, I wish to express my gratitude to Martin Sondermann, Sebastian Severin and Volker Decker. For their support in the identification of macroinvertebrate specimens I am grateful to Armin Lorenz and Peter Rolauffs. Special thanks go to Kathrin Januschke, Caroline Winking, Benjamin Kupilas and Sonja Stendera for proofreading single chapters.

I am grateful to all my colleagues of the working group Aquatic Ecology in Essen. We shared the burden of tackling theses but also had relaxing breaks during the whole PhD time. I wish to thank Caroline Winking, Kathrin Januschke, Elisabeth Müller-Peddinghaus, Sabrina Keil, Kerstin Dangel, Marta von Bertrab, Michelle Keppel, Maria Schröder, Benjamin Kupilas and Veronica Dahm. My special thanks go to Jelka Lorenz for always bringing me back into line when I lost it and for supporting me in facing new challenges in university project management. It has really been a pleasure working with you and I hope that a long friendship will bind us!

For carrying me through the thesis and keeping my mind on the most essential things in life I wish to thank ‘Prinz’ and, of course, Martina and Martin Lenters who have placed so much trust in me.

At least and with all my heart I am thankful for the moral support and the patience of my friends and especially my family. Special thanks to my parents for their endless support and motivation, and for never being tired of guiding me. Your positive attitude kept me going.

Table of Contents

List of Figures

List of Tables

1 Introduction

Species distribution models (SDM) constitute an important tool in applied ecology, biogeography, conservation planning and risk management of terrestrial and aquatic ecosystems, capable of identifying species' habitat requirements and estimating species occurrences based on a set of environmental predictors. In the last two decades SDMs have arrived in several scientific fields like conservation biology and wildlife management in which they obtain information on habitat suitability of unsurveyed locations. For instance, SDMs are extensively used for climate-change related vulnerability assessments (e.g. Peterson et al. 2002, Pearson & Dawson 2003, Thuiller et al. 2005a, Domisch et al. 2011; 2013, Arribas et al. 2012, Kusch 2015). In the face of future environmental changes like climate change or land cover change, SDMs provide the possibility to keep global or even local distribution maps at an actual stage by implementing several prediction scenarios (Franklin 2009). Therefore, SDMs have been applied to project the potential effects of global warming on species distributions and ecosystem properties (Neilson et al. 1992, Pearson & Dawson 2003, Thomas et al. 2004, Botkin et al. 2007, Buisson & Grenouillet 2009, Domisch et al. 2013a). Related to global warming, invasion of non-native species can negatively affect native communities and hence have major ecological and economic impacts (Franklin 2009). SDMs can help determining potential geographic range of an invasive species based on its native range and locations of risk (Peterson 2003, Andersen et al. 2004, Kornis & van der Zanden 2010, Westhoff et al. 2011) and the potential impact of diseases introduced by invasive vectors (Benedict et al. 2007). Beside climate change, multiple other fields of interest have attracted the application of SDMs, such as extinction risk of threatened or endangered species (Ferrier 2002, Wilson et al. 2011, Prié et al. 2014). Also for aquatic ecosystems, SDMs have received increasing attention for conservation of threatened species, e.g. for designating priority areas for coastal vertebrates (Tognelli et al. 2005), protecting endemic headwater fish species in Kentucky, USA (Liang et al. 2012), and freshwater pearl mussels in Sweden (Degerman et al. 2013). Here, SDMs are used to target and prioritize areas for protected status, to design reserves and for risk assessment of those habitats. Moreover, SDMs have been deployed in predicting the potential impacts of global environmental change on biogeographical patterns (Richardson & Whittaker 2010) as well as the impacts of specific anthropogenic stressors like pollution (Tang et al. 2010, Luoto 2011) or land use changes (Lohse et al. 2008, Kristensen et al. 2012, Kopp et al. 2012).

SDMs relate species distribution data (occurrence or abundance at known locations) with information on the environmental and/or spatial characteristics of these locations and predict

species occurrences based on the modelled relationships at different spatial scales (e.g. Elith & Leathwick 2009). Related terms to distribution modelling are ‘bioclimatic envelope modelling’ (Pearson & Dawson 2003, Luoto et al. 2005), ‘predictive habitat distribution modelling’ (Guisan & Zimmermann 2000, Elith & Leathwick 2009), ‘ecological niche modelling’ (Stockwell 2006, Reusser & Lee 2008) or ‘habitat suitability modelling’ (Hirzel & Le Lay 2008, Lock & Goethals 2013). However, ‘species distribution modelling’ is the most widely used term in the context of ecology. The overall ecological research challenge is the determination of environmental gradients along which a species’ response changes. SDMs go one step further by allowing the spatial and temporal extrapolation of a single species occurrence, abundance or even community composition. Based on the niche concept (Hutchinson 1957, Kearney 2006) these statistical methods correlate species’ presences and absences with environmental predictors at those locations. SDMs therefore describe a species’ realized niche using modelling algorithms, based on the given predictors (Domisch 2012). In this way, they contribute to the improvement of understanding the relationship between a species and the environmental conditions observed. Moreover, they predict occurrences or abundances across a landscape, sometimes requiring extrapolation in space and time (Elith & Leathwick 2009). Therefore, SDMs provide an appropriate way to gain information on species occurrences in a catchment without the need to produce catchment-wide and very time- and resource-consuming sampling data. The modelled output may be defined as a probability of occurrence, abundance, physiological or demographic rates within the study area. Especially, valuable information on potential species distributions at the local scale (site), the catchment scale (regional) or even the global scale is derived.

Environmental predictors and species’ spatial records serve as training data for the calibration of a SDM. After selecting the best performing model (for instance, via a coefficient of determination or predictive performance estimated by cross-validation), SDMs provide a spatial map of projected species occurrences or habitat suitability (Figure 1.1). To define a model’s predictive reliability the predictive outcome is then compared to the initial species data (cross-validation) using a resubstitution procedure or it is compared to additional species records that were not included into the model calibration (for example independent survey data or recently collected data).

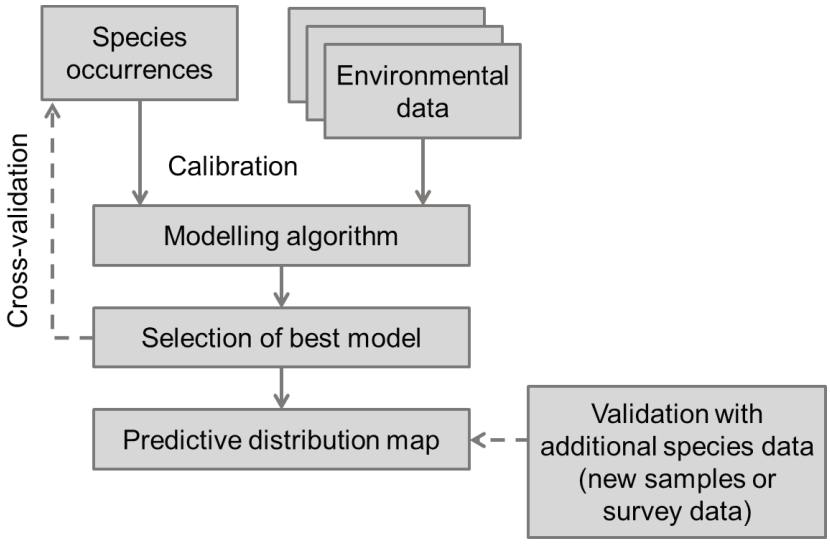

Figure 1.1: General work flow of the species distribution modelling procedure.

Beside the purely academic investigations, the application of SDMs in decision-making policy is still considered critically due to their limitations and basic assumptions (Zurell et al. 2009, Araújo & Peterson 2012). The assumed niche conservatism of species, the lacking consideration of the species adaptation potential, the static nature of the models regarding biotic and abiotic interactions and the tendency to over-simplify complex ecosystems may have contributed to the relatively critical views about SDMs within authorities (Hampe 2004, Pearman et al. 2008, Araújo & Peterson 2012). Especially, SDMs for riverine systems rise specific challenges as rivers are the most heterogeneous ecosystems at small spatial scales (Erös & Schmera 2010). Rivers comprise directional and highly structured networks that are connected laterally, longitudinally and vertically (Ward 1989, Linke et al. 2008). Environmental conditions and ecological processes both in the upstream reaches and the adjacent catchments affect local conditions (Allan 2004, Allen & Vaughn 2010, Jähnig et al. 2012) and thus, the species occurrence and the composition of riverine communities. The riverine habitat structure is nested within a hierarchy of spatial scales, occurring from the surface of individual substrate particles up to entire river catchments (Vaughan et al. 2009). Within this hierarchy, rivers are mosaics of physical habitats, with heterogeneity varying laterally, longitudinally and in relation to stream size (Tockner & Ward 1999, Ward et al. 2002).

Whilst river management efforts have formerly focused on water quality, the improvement in physico-chemical conditions during the last decades disclosed the effects of changes in physical habitat quality and riparian land use conditions on river biodiversity and species occurrences. Due to water abstraction, changes in discharge volumes and riparian agricultural and urban utilization, habitats for species inhabiting river ecosystems have been severely fragmented and desolated. In Europe, these changes have been taken up by the legislative Water Framework Directive (WFD, 2000/60/EC, European Commission 2000). In particular,

the WFD emphasizes the ecological importance of rivers and requires the implementation of assessment programmes to protect or restore 'good ecological status' at all scales from the reach to entire river basins (European Commission 2000). Rivers should be restored to healthy river ecosystems until 2015, assessed by characterizing assemblages of fish, benthic macroinvertebrates and aquatic flora (Hering et al. 2010). With respect to the WFD's targets, a large number of river restoration activities have been installed and the number is still increasing. In 2012, 16% of German river stretches were restored due to the requirements of the WFD while 56% are in the planning or construction phase (BMU 2013). However, hydromorphological restoration does not necessarily lead to strong increase of ecological status. In particular, minor effects of hydromorphological restoration were recorded for benthic macroinvertebrates (Roni et al. 2006, Jähnig et al. 2010, Palmer et al. 2010, Sundermann et al. 2011a). Various reasons for these findings have been discussed: multiple broad-scale stressors like agricultural land use and poor water quality (Palmer et al. 2010, Lorenz & Feld 2013, Sundermann et al. 2013), the length of restored sections, longer time spans needed for recolonization (Lorenz et al. 2009, Bernhardt & Palmer 2011, Parkyn & Smith 2011) and the absence of source populations in the immediate surroundings of the restored sections (Sundermann et al. 2011b, Stoll et al. 2013). In this context, valuable information on species habitat suitability and/or occurrence may be gained by the consultation of SDMs. Once being reliably developed, SDMs may fill gaps of lacking information on potential populations and thus, on stepping stones for restoration success and potential recolonization sources in upstream reaches by providing continuous prediction output. In addition, SDMs allow the computation of hydromorphological or land use scenarios with regard to the estimation of the success of restoration activities on benthic communities and ecological status.

Benthic macroinvertebrates are a widespread, abundant and highly diverse group of organisms who strongly respond to multiple environmental gradients on the species and community level. Many of these gradients are scale related, e.g. catchment vs. habitat-level characteristics (Minshall 1988, Poff 1997). Macroinvertebrate distribution within streams is influenced by various factors at different spatial scales: broad-scale parameters (ecoregion and catchment), fine-scale variables (flow conditions, substrate availability, biotic interactions) as well as interactions between scales (Malmqvist 2002) affect benthic communities. Broad-scale influences originate from hydrological, geomorphological, chemical and agricultural processes in the surrounding environment. For instance, recent studies have shown that benthic communities are affected by hydromorphological conditions (Jähnig et al. 2009, Lorenz & Feld 2013) and upstream land use (Allan 2004, Death & Collier 2010, Feld 2012, Lorenz & Feld 2013). From the very local point of view, fine-scale variables influence benthic communities and single species by the texture of stony surfaces, substrate diversity, existence of rare patchy substrates and mosaic habitat heterogeneity (Beisel et al. 2000, Palmer et al.

2000, Lepori et al. 2005). Different assemblages are associated with riffles and pools, variations in substrate size and the presence of vegetation (Hynes 1970). Moreover, diffuse and local dispersion of substances and topography link the broad-scale influences with local conditions that directly affect aquatic communities.

Ecologists and modellers focus on the determination and prediction of invertebrate distributions according to key environmental factors (Theinemann 1954, Hynes 1970, Townsend & Hildrew 1994, Statzner et al. 2001). This work is still ambitious because environmental factors in streams are embedded in a landscape context (Hynes 1975, Malmqvist 2002, Wiens 2002). SDMs based on broad-scale predictors are commonly linked to scenarios and projections of global species distributions which are related to shifts caused by changing climate, extinction risk (e.g. Araújo et al. 2005, Thuiller et al. 2005a, Buisson & Grenouillet 2009, Domisch et al. 2013b) or species invasions (e.g. Peterson 2003, Thuiller et al. 2005b, Evangelista et al. 2008). However, some authors have successfully investigated SDMs in riverine systems (Buisson & Grenouillet 2009, Prié et al. 2014, Lock & Goethals 2014, DeRolph et al. 2015), but further efforts in extrapolating species occurrence continuously along river courses across entire catchments are still in an early stage (Domisch et al. 2015).

Scope of this thesis

The objectives of this thesis were the development and testing of the applicability of SDMs on stream macroinvertebrates based on broad-scale environmental predictors in terms of generality and predictive success. Broad-scale variables (land use and physical habitat quality) that are continuously available throughout riverine systems could therefore constitute easily applicable surrogate predictors to forecast instream macroinvertebrate distribution along river courses. During two extensive sampling campaigns, species data and a variety of broad- and fine-scale environmental data were collected. These data were used to describe the species ecological requirements in detail (chapter 3). SDMs were trained on land use variables and physical habitat quality and then compared to SDMs including additional fine-scale variables to assess the appropriateness of broad-scale SDMs (chapter 4). By developing SDMs separately for adjacent watersheds the model's predictive output was extrapolated and validated on river sections beyond the region the models were trained on (chapter 4). The analysis addressing the appropriate validation of macroinvertebrate SDMs was based on the data separation by sampling year, providing a direct verification of SDM predictions by related field data (chapter 5). The species prevalence was considered to potentially affect the SDM performance in both spatially and temporally separated analyses (chapter 4 and 5).

The aims and related hypotheses (H) of this thesis were:

1. the detailed description of the species' actual distribution and the determination of their ecological requirements including a literature cross-check (chapter 3)

2. testing the applicability of distribution models based on broad-scale predictors and the comparison to models using fine-scale predictors (chapter 4)

   H2a: SDMs based on broad-scale predictors as proxies for local conditions achieve acceptable performance.

   H2b: The inclusion of local, fine-scale predictors like physico-chemical variables and substrates lead to a significant improvement of SDM performance.

3. testing the transferability of the model's spatial predictions to adjacent regions (chapter 4)

   H3: SDM predictions for adjacent watersheds based on the same environmental data are spatially transferable due to the similar environmental characteristics of both watersheds.

4. properly validating distribution models using different data sets for validation (chapter 5)

   H4: Validating SDM predictions by a new field campaign (field validation) obtains a more realistic assessment of SDM predictive performance than internal cross-validation or using independent survey data alone.

5. determining the effect of species prevalence on the model's performance (chapters 5, partly discussed in chapter 4)

   H5: SDMs of less prevalent species tend to over-predict species absences rather than presences.

2 Materials and Methods

2.1 Study area

The study area is located in the mountainous catchment of the River Ruhr in Western Germany, Europe, (altitude: 100–720 m a.s.l.) and consists of two major watersheds of similar expansion (Figure 2.1). Until the confluence with the Lenne, the Upper Ruhr river is 126 km long with a drainage area of 2,100 km^2. The river Lenne has a length of about 129 km and drains 1,352 km^2. The entire watershed has a siliceous geology (mainly shist) and is characterized by cobble- and pebble-bed streams. Two different river types are dominant in the study area: small siliceous highland rivers dominated by coarse substrates (river type 5, Figure 2.2 A + C) and mid-sized to large siliceous highland rivers dominated by fine to coarse substrates (river type 9 and 9.2, see Figure 2.2 B + D) according to Pottgiesser & Sommerhäuser (2008). The river Ruhr as well as the river Lenne have their sources near Winterberg, North Rhine-Westphalia. Land cover is dominated by non-native coniferous forest and remnants of natural deciduous forest at the hillslopes, with agriculture and urbanization mainly occurring in larger valleys. After several decades of heavy pollution, the water quality of the entire watershed increased and reached a good status (Ruhrverband 2009, 2013) unlike hydromorphology, which is degraded in large parts of the watershed due to water abstraction, impoundments, bank and bed fixation and riparian modification (LUA & MUNLV 2005, MUNLV 2005).

The watersheds Lenne and upper Ruhr were selected as I suggested similar species occurrences due to the fact that they are located in the same mountainous region. The sub-watersheds Bigge (Lenne) and Moehne (Ruhr), highlighted in grey in Figure 2.1, were excluded from any further analyses as their hydromorphology and water quality are known to be highly influenced by large retaining lakes.

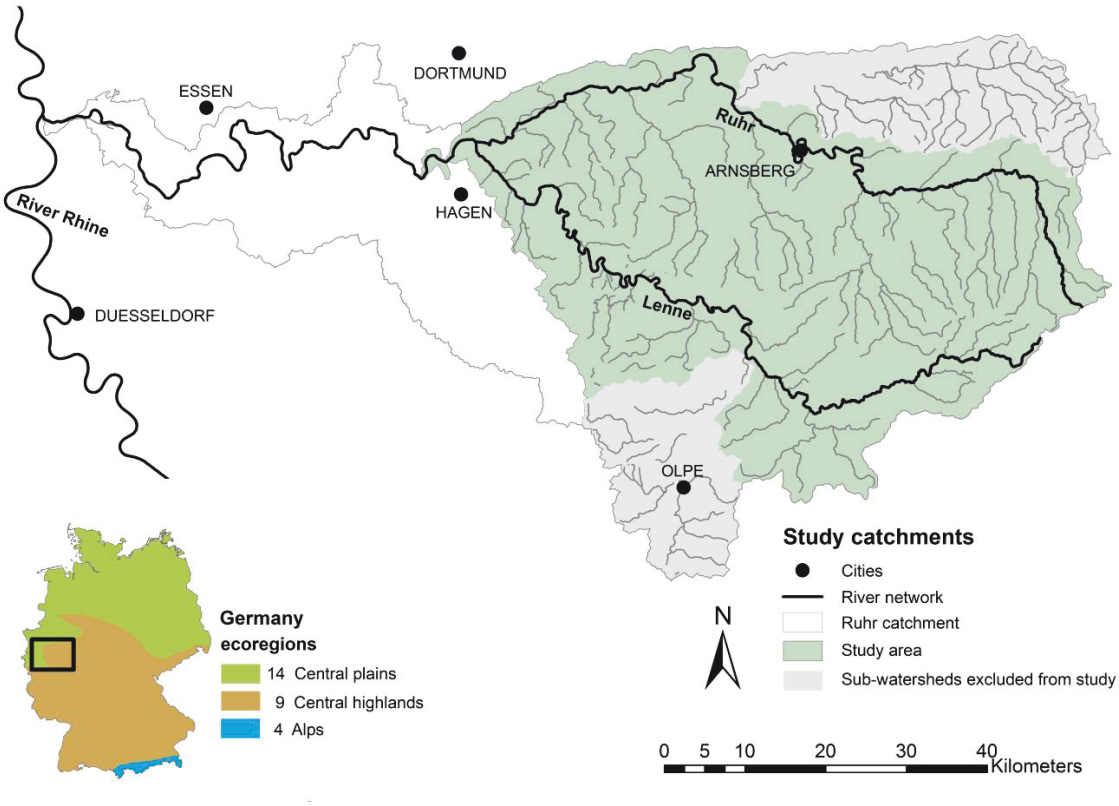

Figure 2.1: Study area including two watersheds Lenne and Ruhr. The Lenne watershed is the main tributary of the Ruhr which flows into the Rhine at Duisburg. The grey sub-watersheds represent the Bigge (Lenne) and Moehne (Ruhr) watersheds that were excluded from this study because of hydromorphological and water quality impacts caused by reservoir lakes in the continuum.

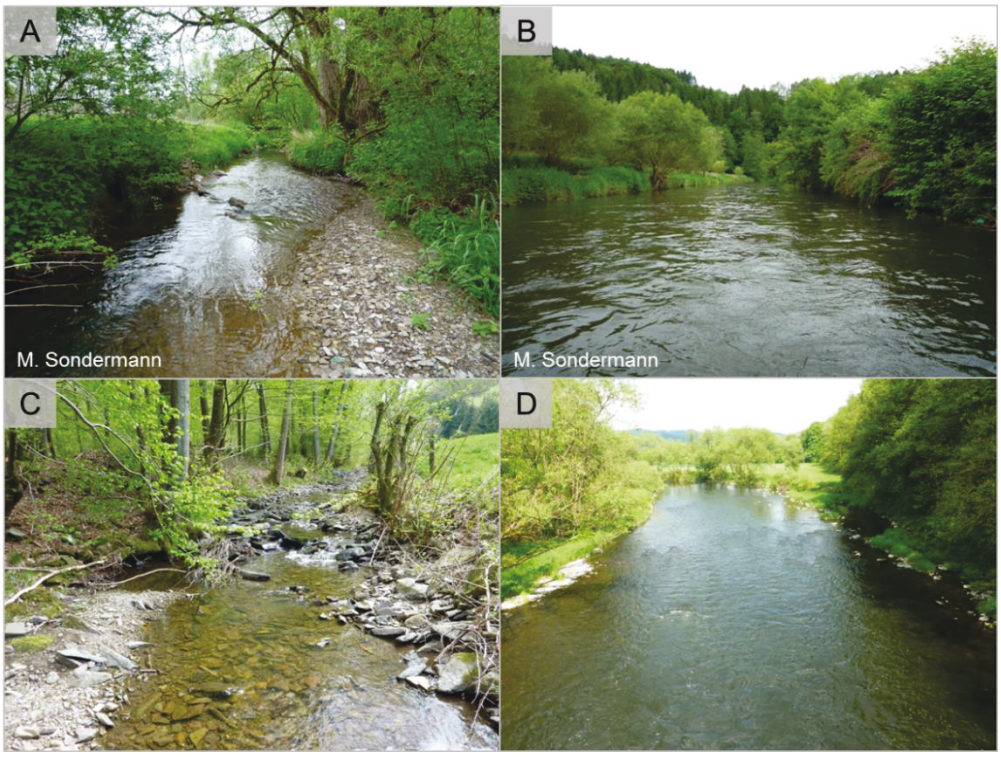

Figure 2.2: Examples of sampling sites in the Lenne and Ruhr watershed: A Hellefelder Bach (Ruhr watershed, river type 5), B Ruhr at Meschede (river type 9), C Nahmer Bach at Hobräck (Lenne watershed, river type 5), D Lenne at Pasel (river type 9).

2.2 Model species

For distribution modelling, eleven model species were selected (Table 2.1). These species had to meet several criteria: a frequency of occurrence (prevalence) of 5 – 60% in both Lenne and Ruhr watersheds turned out from available federal survey data on macroinvertebrate biocenosis' (provided by the North Rhine-Westphalia State Agency for Nature, Environment and Consumer Protection, LANUV), sensitivity to hydromorphology (positive German Fauna Index), habitat specificity and relevance to the German river assessment method PERLODES (Hering et al. 2004, Meier et al. 2006). The sensitivity to hydromorphology was assessed by the species' classification into the German Fauna Index that describes the effects of morphological degradation on the invertebrate fauna of a stream section based on stream type specific indicator lists (Lorenz et al. 2004, Meier et al. 2006). Indicator values range between -2 (taxa of morphologically degraded streams) and +2 (taxa mainly occurring in morphologically intact streams). Model species in this study matched positive indicator values.

Chapter 3 gives details on the ecological preferences and spatial distribution of the model species.

Table 2.1: Selected macroinvertebrate model species, their genus and abbreviations used in this study.

Genus	Species	Abbreviation
Crustacea, Amphipoda	*Gammarus pulex* (LINNAEUS, 1758)	Gampul
Ephemeroptera	*Siphlonurus lacustris* (EATON, 1870)	Siphlac
Odonata	*Calopteryx virgo* (LINNAEUS, 1758)	Calvir
Plecoptera	*Leuctra geniculata* (STEPHENS, 1836)	Leugen
	Dinocras cephalotes (CURTIS, 1827)	Dincep
	Perla marginata (PANZER, 1799)	Permar
Trichoptera	*Silo pallipes* (FABRICIUS, 1781)	Silopall
	Silo piceus (BRAUER, 1857)	Silopic
	Hydropsyche dinarica MARINKOVIC, 1979	Hyddin
	Hydropsyche incognita PITSCH, 1993	Hydinc
	Hydropsyche instabilis (CURTIS, 1834)	Hydins

2.3 Selection of sampling sites and sampling methodology

Sampling of macroinvertebrate species was carried out during spring season (April – mid of June) in the years 2010 and 2011. Sampling site selection was stratified by river typology to

ensure representativeness and river size homogeneity within the data set. In 2010, sample sites were selected randomly for the three different river types (small water bodies near to the source (without typology), small siliceous highland rivers dominated by coarse substrates (type 5) and mid-sized to large siliceous highland rivers dominated by fine to coarse substrate (type 9/9.2)) based on a river network providing river sections of 100 m in length. In 2011, random site selection was additionally stratified according to the predicted presences and absences based on SDMs on the 2010 data. This ensured a balanced coverage of predicted presences and absences of model species in the final validation data set.

In spring 2010, 60 sample sites in the Lenne watershed and 61 sample sites in the Upper Ruhr watershed were sampled. In 2011, 52 Lenne sites and 52 Ruhr sites were additionally sampled. Thus, 112 Lenne sample sites and 113 Ruhr sample sites including information on presences/absences of all model species have been gathered for distribution modelling (Figure 2.3). The sampling sites covered 147 type 5 reaches (65.3%), 5 type 7 reaches (2.2%), 50 type 9 and 9.2 reaches (22.2%) and 23 reaches without typology (10.2%) due to their small catchment size < 10 km^2.

At each sample site, macroinvertebrate larvae were collected for 45 minutes using a standard hand-net (frame: 25 x 25 cm, mesh size: 500 µm) and a multi-habitat technique. All habitats known to be relevant to the species' occurrence as reported in the literature were thoroughly inspected for 45 minutes within a 100 m sampling section in order to reduce the record of false absence, i.e. overlooked species (type I sampling error). Up to ten samples per habitat were thoroughly inspected to account for the potential patchiness of the distribution of the species. This sampling method was selected to cover those species known to be highly sensitive and habitat specific. All specimens were pre-sorted on site, preserved in 80% Ethanol and identified in the laboratory using identification keys as indicated in Table 2.2.

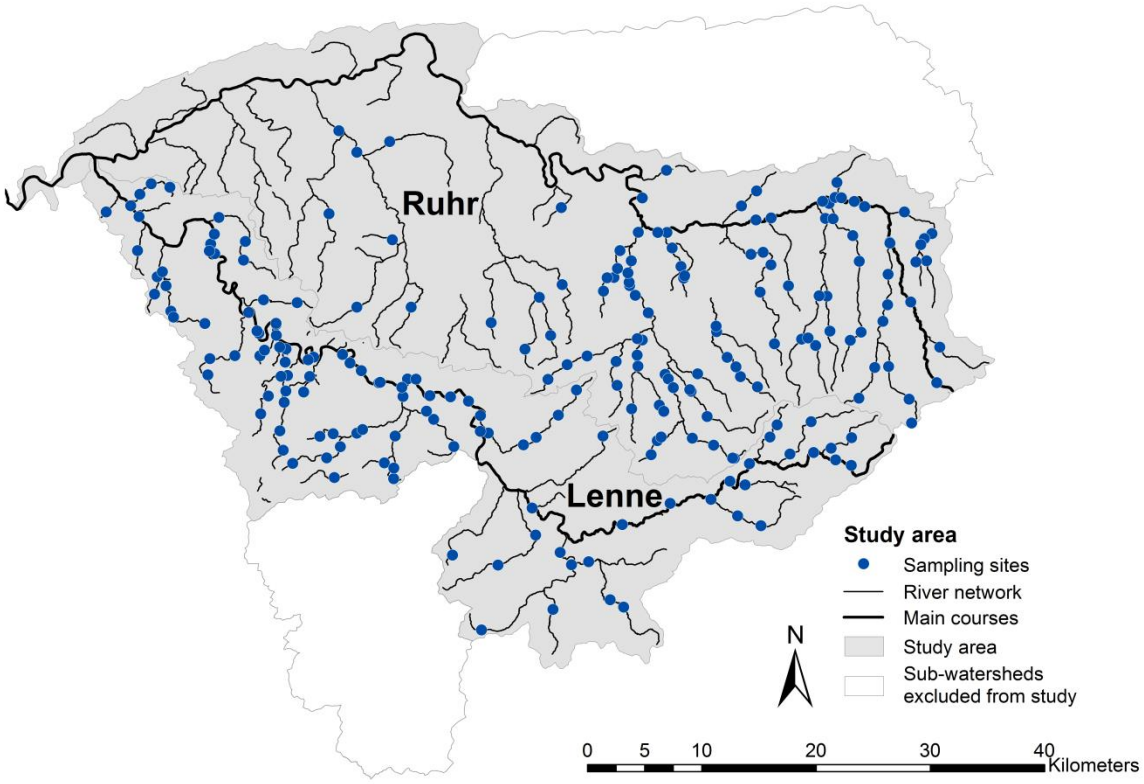

Figure 2.3: Sampling sites in the study area. Sampling sites are indicated by points.

Table 2.2: Identification keys used to specify species level (Lv.: Larvae; Ad.: Adults).

Genus	Reference
All genera	Bayerisches Landesamt für Wasserwirtschaft (1992). Bestimmungsschlüssel für die Saprobier-DIN-Arten (Makroorganismen). Informationsberichte Heft 2/88, 274pp.
Crustacea, Amphipoda	Eggers, T.O. & A. Martens (2004). Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands. Lauterbornia 42, 68pp. Eggers, T.O. & A. Martens (2007). Ergänzungen und Korrekturen zum "Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands". Lauterbornia 50, 1-13.
Ephemeroptera (Lv.)	Eiseler, B. (2005). Bildbestimmungsschlüssel für die Eintagsfliegenlarven der deutschen Mittelgebirge und des Tieflands. Lauterbornia 53, 112pp. Studemann, D., P. Landolt, M. Sartori, D. Hefti & I. Tomka (1992). Insecta Helvetica. Fauna. 9. Ephemeroptera. Hrsg. Schweizerische Entomologische Gesellschaft, Redakteur: Sauter
Trichoptera (Lv.)	Waringer, J. & W. Graf (1997). Atlas der österreichischen Köcherfliegenlarven unter Einschluß der angrenzenden Gebiete. Facultas-Universitätsverlag: 286p. + Ergänzungen und Berichtigungen zum Atlas der österreichischen Köcherfliegenlarven unter Einschluß der angrenzenden Gebiete (2004). Fakultas-Universitätsverlag, 28pp. Pitsch, T. (1993). Zur Larvaltaxonomie, Faunistik und Ökologie mitteleuropäischer Fließwasser-Köcherfliegen (Insecta: Trichoptera). Landschaftsentwicklung und Umweltforschung - Schriftenreihe des Fachbereichs Landschaftsentwicklung der Technischen Universität Berlin. Sonderheft S8, 316pp. Edington, J.M. & A.G. Hildrew (1995). Caseless caddis larvae of the British Isles (with notes on their ecology). Freshwater Biological Association Scientific Publication No. 53. Neu, P.J. & W. Tobias (2004). Die Bestimmung der in Deutschland vorkommenden Hydropsychidae (Insecta: Trichoptera). Lauterbornia 51, 68pp. Malicky, H. (2004). Atlas of European Trichoptera. Second Edition. Springer Verlag, 359pp.
Trichoptera (Ad.)	Tobias, W. & D. Tobias (1981): Trichoptera Germanica - Bestimmungstafeln für die deutschen Köcherfliegen Teil I Imagines. Courier Forschungsinstitut Senckenberg 49, Frankfurt a.M. Neu, P.J., <http://www.trichoptera-rp.de/html/taxonomie.html>
Plecoptera (Lv.)	Zwick, P. (2004). Key to the West Palaearctic genera of stoneflies (Plecoptera) in the larval stage. Limnologica 34, 315-348.
Odonata (Lv. und Ad.)	Bellmann, H. (1993, 2007). Libellen: beobachten – bestimmen. Naturbuch-Verlag, Augsburg. Bellmann, H., 2007. Der Kosmos-Libellenführer: Die Arten Mitteleuropas sicher bestimmen. Franckh-Kosmos-Verlag, Stuttgart, 320pp. ISBN: 978-3-440-13516-7

2.4 Environmental data

2.4.1 Broad-scale variables

Hydromorphological variables were derived from the national hydromorphological survey (LAWA 2000, briefly described by Raven et al. 2002, Kail & Hering 2005) for those 100 m sections, in which sites were located. The national hydromorphological survey provides a data collection that helps to define degradation status of a particular river stretch and to determine potential ecological deficits. Assessment scores of altogether 25 single habitat variables (Table 2.3 and Appendix 1d) were available for each 100 m section within the entire study area, ranging from classifications 1 (no alteration) to 7 (complete alteration). The survey also provides stream size characteristics (local situation, mean water depth, stream type, channel size etc.) and four additional scores about special stressors at that local site. Table 2.3 gives information about the classification levels in physical habitat quality assessment in Germany. If an assessment of attributes was not possible, the value of those parameters was set to zero.

Land use data were used to describe the overall catchment characteristics and the potential influence of stressors like urbanization and agricultural land use on the occurrence of the model species at the respective sampling site. Catchment land use for each site was derived from the ATKIS land cover vector data (ATKIS 2007). Data on land use in the study area were compiled for all sampling sites using Geographic Information System (GIS) tools in ArcGIS (ESRI 2011). Unlike CORINE, the ATKIS data are vector data delineating areas of homogeneous land cover. The fine resolution allowed determining percent land use within two 1 km long buffer areas upstream of each sampling site. Buffer width was 10 m and 100 m on each bank side of a stream (Table 2.4). Technically, this was implemented by clipping buffer polygons with ATKIS land use vector maps in ArcGIS (ESRI 2011). ATKIS provides 36 single land use categories for the study area which were aggregated to five major land use classes: intensive (cropland) and extensive agriculture (e.g. meadow, pasture), deciduous and coniferous forest, urban/industrial areas and infrastructure (Appendix 1e). The quotient of total percent forest in the 20 m wide buffer and percent urban area and cropland in the 200 m buffer (variable code: F020U200) (Table 2.4) was additionally introduced. Thereby, I account for the potential buffer capacity concerning upstream physicochemical stress (Feld et al. 2011). The index ranges from 0 to infinity, with index values >1 indicating a high potential buffer capacity, for instance, against pollution and sediment input. The upstream riparian buffer capacity is low (F020U200 < 1.0) because of high percentage of intensive land use and material load. If F020U200 > 1.0, a riparian woody buffer leads to a higher upstream buffer capacity and less material stress.

Finally, the distance to source (m) and the altitude a.s.l. (m) were generated for the upstream edge of each sample section to account for the natural variability inherent to the stream size and altitude (temperature) gradients in the model catchment.

Table 2.3: Parameters on physical habitat quality. Parameters which were included into the distribution models in chapter 4 and 5 are marked with an asterisk. For detailed information on the data scale see Appendix 1d.

	Physical habitat parameter	**Abbreviation**
	Total hydromorphological assessment score	GSG_I
Stream character-istics	Local situation (urban/landscape) *	LocSit
	Mean water depth *	MWD
	Urbanisation level	URB
Channel pattern	Planform *	Form
	Erosion at bends *	Erosion
	Bars *	Bars
	Features indicating natural channel dynamics (e.g. wood jams, island, widening) *	FeatDyn
Longitudinal profile	Artificial barriers (dams, weirs) *	ArtBarr
	Culverts	Culverts
	Artificial impoundments	ArtImp
	Riffles and steps *	Riffles
	Flow diversity *	FlowDens
	Depth variability *	DepVar
	Flow pattern	FlowPatt
Channel bed features	Substrate * (dominant)	Substr
	Bed-fixation	BedFix
	Substrate diversity *	SubsDiv
	Channel features (e.g. scour- and backwater pools, rapids, cascades) *	FeatChan
	Macrophytes	Macroph
	Features indicating channel stress/pressures	ChanStress
Cross section	Cross-section form *	CrSecForm
	Cross-section depth *	CrSecDep
	Bank erosion * (indicating widening of channel)	BankEro
	Cross-section width variability	CrSecWid
	Bridges	Bridges
Channel bank features	Riparian vegetation *	RipVeg
	Bank protection *	BankProt
	Bank features * (e.g. woody debris, undercut banks)	FeatBank
	Features indicating riparian stress	RipStress
Floodplain	Land-use *	Landuse
	Riparian buffer strip *	RipBuff
	Infrastructure works (e.g. roads, dumping sites, fish-farms) *	Infrastruc
	Riparian Features	FeatRip

Table 2.4: Overview on land use categories in two different buffer sizes related to the river network. Water bodies were excluded as percentages of water bodies mainly include the stream bed itself or lakes the streams are flowing through.

Land use category	Buffer size	Scale	Abbreviation
Cropland	10 m on either bank side (narrow)	%	Crop_n
	100 m on either bank side (wide)	%	Crop_w
Extensive / pasture	10 m on either bank side (narrow)	%	Ext_n
	100 m on either bank side (wide)	%	Ext_w
Deciduous forest	10 m on either bank side (narrow)	%	DecFor_n
	100 m on either bank side (wide)	%	DecFor_w
Coniferous - mixed forest	10 m on either bank side (narrow)	%	ConFor_n
	100 m on either bank side (wide)	%	ConFor_w
Urban/industrial area	10 m on either bank side (narrow)	%	Urb_n
	100 m on either bank side (wide)	%	Urb_w
Ratio %forest in 200 m buffer to %urban in 20 m buffer		>0.0	F020U200

2.4.2 Local (fine-scale) variables

Physico-chemistry and coverage of bottom substrates were recorded at each sampling site during the field campaigns in 2010 and 2011 (Table 2.5). Coverage of river bottom substrates was recorded in 5% intervals according to the multi-habitat sampling procedure described by Hering et al. (2003). These microhabitats cover mineral (macro- to microlithal, gravel, sandy to loamy substrates) and organic substrates (coarse and fine particulate organic matter, wood, roots, macrophytes) at the river bottom and bank sides. To determine those reaches with strongly polluted conditions, measurements of physicochemical parameters like water temperature (°C), pH, conductivity (µS/cm), oxygen saturation (%), chloride, phosphate, ammonium and nitrate content (mg/l) was accomplished using several standard devices (Greisinger GLM 020A for water and air temperature and conductivity, WTW ProfiLine Oxi 3210 for oxygen, WTW 315i for pH). Merck rapid tests based on titration were used to determine nitrate, nitrite, ammonium, phosphate, chloride contents and hardness.

Additional to the hydromorphological survey protocol (LUA 1998) a detailed field protocol (Appendix 1a) was designed incorporating valuable information on number and characteristics about river bed structures, dead wood, colmation, shaded areas, bank reinforcement at the sampling site and upstream sections, number and characteristics of transversal structures, impoundments and residual water sections, flow velocity and flow depth.

Table 2.5: Local (fine-scale) environmental variables on physico-chemical and substrate variables. Microhabitat classification and description is based on substrate types according to multi-habitat sampling protocol (Hering et al. 2003).

Physico-chemical and substrate variables		**Scale**	**Abbreviation**
Water temperature		°C	T_water
Conductivity		µS cm^{-1}	Cond
Oxygen content		mgl^{-1}	O2_cont
Oxygen saturation		%	O2_sat
pH			pH
Nitrate		mg l^{-1}	NO3
Nitrite		mg l^{-1}	NO2
Ammonium		mg l^{-1}	NH4
Chloride		mg l^{-1}	Chloride
Phosphate		mg l^{-1}	PO4
Carbonat hardness		mmol l^{-1}	Carb_H
Total hardness		mmol l^{-1}	Total_H
Macrolithal (>20 - 40cm)	Large cobbles, boulders and blocks, bedrock; coarse blocks, head-sized cobbles, with a variable percentages of cobble, gravel and sand	%	Macro
Mesolithal (>6 - 20cm)	Fist to hand-sized cobbles with a variable percentage of gravel and sand	%	Meso
Microlithal (>2 - 6cm)	Coarse gravel (size of a pigeon egg to child's fist) with variable percentages of medium to fine gravel	%	Micro
Akal (>0,2 - 2cm)	Fine to medium-sized gravel	%	Akal
Psammal/Psammopelal (>6µm - 2mm)	Sand	%	PsammPel
Argyllal (<6µm)	Silt, loam, clay (inorganic)	%	Argyll
Technolithal	Artificial, head-sized cobbles	%	Tech1
Algae	Filamentous algae, algal tufts	%	Algae
Macrophytes	Submerged and emergent macrophytes	%	MP
Living parts of terrestrial plants	e.g. fine roots, floating riparian vegetation	%	LTTP
Xylal	Dead wood and tree trunks	%	Xylal
CPOM	Deposits of coarse particulate organic matter, e.g., fallen leaves	%	CPOM
FPOM	Deposits of fine particulate organic matter, e.g., mud und sludge (organic)	%	FPOM

2.5 Distribution modelling and statistical evaluation

2.5.1 Non-parametric multiplicative regression (HyperNiche)

The species distribution models were built using nonparametric multiplicative regression (NPMR). This regression method finds increasing application to the field of ecology, especially in determining relations between environment and species occurrence. NPMR has been applied mainly in vegetation ecology (e.g. McCune 2007, Ponader & Potapova 2007, Yost 2008, Giordani & Incerti 2008, Schroeder et al. 2010, Shrestha et al. 2012) and, since a few years, it is in use for modelling macroinvertebrates (Free et al. 2009, Jyväsjärvi et al. 2011, Scherr et al. 2011). NPMR is based on kernel functions to weight observations and can be applied in both a niche identifying and predictive way (McCune 2009). The NPMR technique is applicable for many dimensions in predictor variables. The multidimensionality is provided multiplicatively so that complex interactions among predictors are automatically incorporated into the models (McCune 2006, McCune 2009). NPMR can be applied to either presence-absence or quantitative response data.

The NPMR approach uses a Gaussian kernel function for iterative, forward stepwise search of those combinations of environmental variables that explains the presence/absence of the model species the most (McCune 2006, McCune & Mefford 2009). The distance-weighted Gaussian smoothing function gives full weight (1.0) to those observations with exactly the same environment as the optimal target point and diminishes weight to zero with increasing distance to the target point (McCune 2006, McCune 2009). This relationship between weight and distance to the target point is named ‘local mean model’ (McCune & Mefford 2009).

In the analyses, I used two measurements to evaluate model performance that is the strength of the species-environment relationship: the pseudo-R-squared (xR^2) and the log likelihood ratio (logB). The common method of evaluating model performance is a pseudo-R-squared (xR^2) statistic which is calculated by the size of the residual sum of squares in relationship to the total sum of squares. xR^2 is equivalent to the to the traditional R^2 value, but has no fixed lower bound, so that negative values are possible (McCune 2009). In this study model fit is also described by a log likelihood ratio logB that can be interpreted as the ratio of the likelihood of cross-validated estimates from the fitted model to estimates from the naïve model expressed in powers of ten. A naïve model is simply that the best estimate of the probability of encountering a species in a study area is the average frequency of occurrence of that species in the data. LogB is derived from cross-validated estimates using a leave-one-out strategy. This cross-validation compares the predictive model output to the initial species data used for model training, applying a resubstitution procedure. k – 1 subsamples are used as training data and the remaining subsample is used as validation data for testing the model (Kohavi 1995). The procedure is repeated k times (k-fold), i.e. each of the k subsamples is left out once

and used for validation (Hastie et al. 2001, Arlot & Celisse 2010). LogB is dimensionless and takes negative values when cross-validated estimates from the fitted model are worse than the null model and increases with strength of the modeled relationship between species and environmental variables (McCune 2006, McCune & Mefford 2009).

Sensitivity of each model predictor was measured by nudging the observed values up and down by 5% of the range of individual predictors, and calculating the resulting change in the estimate for that point (McCune 2006, McCune 2007). By accumulating those sensitivities across all data points, one can evaluate the sensitivity of the model to each predictor. The greater the sensitivity, the more influence the predictor variable has in the model. A sensitivity value of 1.0 means that a 10% change in the predictor would produce a 10% change in the response (McCune 2006).

The modelling procedure was performed with the HyperNiche software version 2.20 (McCune & Mefford 2009). The NPMR modelling method was applied using a default minimum average neighborhood size (N*) of 5% of the total sampling units (number of sites * 0.05) as limit to accept (N*>0.05) or reject (N*<0.05) a model. N* is the average sum of the weights for other data points that bear on the target point. Neighbourhood size can be defined as the sum of weights or amounts of data used to calculate the estimated response at any given point, and the average neighbourhood size is the sum of neighbourhood sizes for all points divided by the total number of points. This value decreases with the increase in number of variables (Yost 2008). The minimum neighborhood size for an estimate therefore controls how broadly a model is extrapolated in the predictor space avoiding estimates of a response in a region of the predictor space with insufficient data.

2.5.2 Logistic binary regression (SPSS)

Logistic binary regression (LR) is most useful for modelling the relationship between a nominal response variable with two outcomes (binary) and one or more independent variables that are of arbitrary scale. LR belongs to the additive regression techniques and constitutes a quasi-standard for the regression of binary (nominal) response variables against ordinal or continuous predictor variables. Forwards elimination was applied to select the variables in the final models. Regression coefficients were tested by the Wald statistic. A variable is useful to the model if the Wald statistic is less than 0.05. The logistic regression modelling was performed using the Software SPSS Statistics version 20 (IBM 2011).

The model performance (goodness-of-fit) of a logistic regression model is described by Nagelkerke's pseudo-R^2 (Nagelkerke 1992) that is an adjusted version of the Cox & Snell R^2 based on maximum likelihood estimation. The logistic model's goodness-of-fit was tested by the Hosmer-Lemeshow statistic which sorts observations in increasing order of their estimated

event probability into ten groups and tests for significant differences between observed and estimated values giving significance if differences are small. Thus, the Hosmer-Lemeshow statistic indicates a poor fit if the significance value is less than 0.05. However, xR^2 and Nagelkerke's R^2 are equivalent to the linear R^2 describing the ratio of explained variance of the model.

2.5.3 Predictive maps

Continuous prediction probabilities from SDM models may be interpreted i) as habitat suitability, i.e. the percentage to which the habitats at a particular site correspond to the species habitat requirements (as estimates of the probability that species might find suitable habitat in a given area (Araújo & Williams 2000), or ii) as probabilities of occurrence, i.e. estimates of the likelihood that a species might occur at a given unrecorded location (Segurado & Araújo 2004). In my analyses, I followed the latter definition by Segurado & Araújo (2004).

The prediction feature was applied on the regional river network which is provided by the physical habitat survey. Both watersheds cover in total 10,701 river sections in 100 m in length. Small and medium sized rivers (type 5) comprehend in total 10,342 sections; streams comprehend 359 sections (main course of Lenne and Ruhr). I used the best model to estimate the response variable within the respective watershed. For each new site, e.g. 100 m section, probabilities of occurrence (values between 0 and 1) were produced for each model species in consideration of the given predictor variables. These estimates can also be interpreted as the percentage of habitat suitability within this river section. Finally, predictive maps were generated in ArcGIS 10 taking into account the species-specific subsampled range in distance to source.

The NPMR technique allows a prediction of a species‘ probability of occurrence at new sites with given environmental variables. While LR produces consistent predictions for each river section, NPMR assigns a missing value (NA) instead of an estimate of probability if the neighborhood size of this sampling point is smaller than the criterion minimum (set to 25% of the average neighborhood size).

2.6 Model validation

2.6.1 Threshold-dependent performance measures

To adequately test the predictive performance, i.e. the reliability of the given SDM predictions, it is recommended to compare the prediction output of the model to observed presences/absences of a species. This comparison may be based on the model input data set for species' presences/absences, but also on different data sets providing species observations (in consideration of similar sampling methods and time periods). The assessment of the predictive performance is based on threshold-dependent or -independent measures. By translating continuous predictive output of a model into binary values coherent to the presence/absence of a species, predictions and observations can be compared. This requires the definition of a threshold at which the predictive values are split into absence and presence. In my analyses, a threshold of 0.5 was chosen to create threshold-dependent measures as outcome of a 2x2 confusion matrix. Such confusion matrices compare the observed presences/absences to the predicted presences/absences by the calculation of four descriptive values (Table 2.6). True positives (TP) indicate the number of correctly classified presences out of all observed presences. True negatives (TN) indicate the number of correctly classified absences out of all observed absences. False positives (FP) indicate the number of incorrectly classified absences out of all observed absences. False negatives (FN) indicate the number of incorrectly classified presences out of all observed presences (Fielding & Bell 1997, Fawcett 2006).

Table 2.6: Elements of a confusion matrix as the basis for predictive performance measures according to Fawcett (2006).

		Observation	
		present	absent
Prediction	present	true positive (TP)	false positive (FP)
	absent	false negative (FN)	true negative (TN)
	Total (N)	P	A

Beside the above mentioned components of a confusion matrix, I used 3 threshold-dependent performance measures to evaluate the predictive performance of the models. First, the percent of true and false prediction (% of TP, TN, FP, FN) were calculated. Second, the accuracy or percent correctly classified (PCC) is the overall correct classification rate, in terms of the proportion of all correctly classified predictions compared to the total number of predictions (Table 2.7 no. 2). Third, Allouche et al. (2006) introduced another predictive performance

measure, the true skill statistic (TSS). The TSS compares the number of correct predictions, minus those attributable to random guessing, to that of a hypothetical set of perfect predictions (Table 2.7 no. 3). By summing up sensitivity and specificity TSS takes into account both omission and commission errors, and success as a result of random guessing, and ranges from −1 to +1, where +1 indicates perfect agreement and values of zero or less indicate a performance no better than random. Allouche et al. (2006) stated that the TSS is independent of prevalence whereas the Kappa statistic responds to prevalence in an unimodal pattern.

Table 2.7: Threshold-dependent performance measures of a model's predictive performance derived from a confusion matrix.

No.	Performance criteria	Formula
1	Prevalence	p = P / N
2	Accuracy = Percent Correctly Classified	PCC = (TP+TN) / N
3	True skill statistic	TSS = (TP / P) + (TN / A) -1 = Sens + Spec - 1
4	Sensitivity	Sens = TP / P
5	Specificity	Spec = TN / A

2.6.2 Threshold-independent performance measures

Receiver Operating Characteristics (ROC), initially originating from signal detection theory (Kraemer 1988), were developed to define diagnostic test performance, independently of chosen cut-off threshold and prevalence (e.g. Robertson & Zweig 1981, Van Steirteghem et al. 1982, Robertson et al. 1983; Zweig et al. 1992, Zweig & Campbell 1993, Park et al. 2004), but is now used as a standard measurement of SDM accuracy (e.g. Pearce & Ferrier 2000, Manel et al. 2001, Jiménez-Valverde 2012). This method provides an estimation of model accuracy (Zweig & Campbell 1993, Fawcett 2006) by the calculation of confusion matrices for a predefined number of thresholds which split the probabilities of occurrence into a binary data set (subgroups). The ROC plot is based on the calculation of the sensitivity (true positive rate, Table 2.7 no. 4) and specificity (false positive rate, Table 2.7 no. 5). The sensitivity describes the percentage of correctly classified presences compared to the observed presences. The specificity describes the percentage of correctly classified absences compared to the observed absences (Fawcett 2006). The ROC plot is a graph of all sensitivity/specificity pairs resulting from continuously varying probability thresholds. On the y-axis sensitivity is depicted, on the x-axis 1 – specificity is plotted (Figure 2.4). Good predictive performance is characterized by a curve that maximizes sensitivity for low values of (1 – specificity), i.e. when the curve passes close to the upper left corner of the plot (Robertson et al. 1983). High performance models are

indicated by large areas under the curve (AUC). AUC values are used as a single threshold- and prevalence-independent measure for predictive performance (e.g. Manel et al. 2001, Thuiller 2003, Brotons et al. 2004, McPherson et al. 2004, Elith et al. 2006, Kleinwächter & Rickfelder 2007, Moilanen et al. 2008). The AUC is a non-parametric statistic for measuring discriminatory ability of SDMs, i.e. for the ability of a model to correctly distinguish between sites where a species is present versus those where it is absent (Hanley & McNeil 1982, Vaughan & Ormerod 2005). AUC values of 0.5 indicate performance no better than random (Figure 2.4). Usually, AUC values of 0.5 – 0.7 imply low predictive discrimination, values of 0.7 – 0.9 indicate useful applications and values of > 0.9 indicate nearly perfect discrimination (Swets 1988). Elith et al. (2006) used a cut-off of AUC = 0.75 for models that had "a useful amount of discrimination". In this study I followed Araújo et al. (2005) interpreting AUC range values ≥ 0.90 as excellent, 0.80 – 0.90 as good and 0.70 – 0.80 as fair predictive performance (see also Swets 1988).

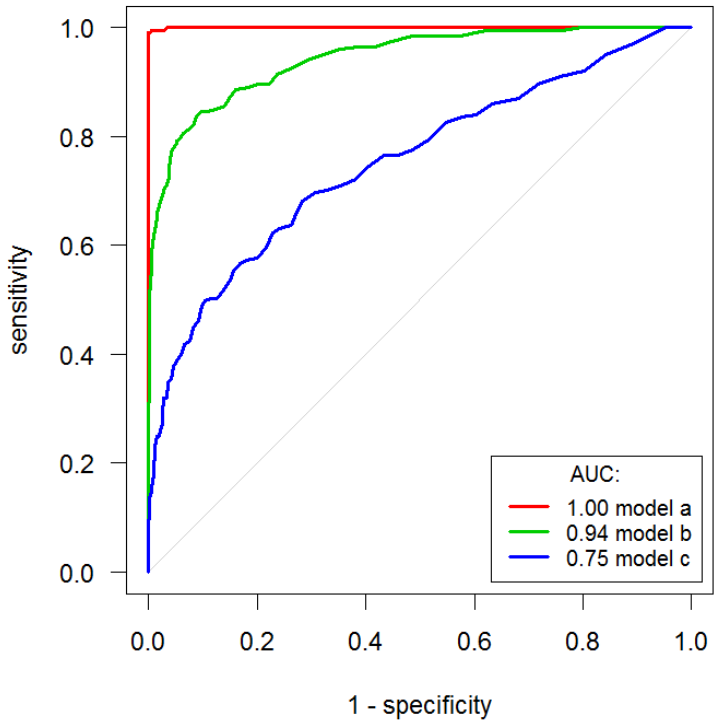

Figure 2.4: An example of a receiver-operating characteristic (ROC) curve. Good predictive performance is characterized by a curve that passes close to the upper left corner of the plot (Robertson et al. 1983), i.e. which maximizes the area under the curve.

Sensitivity and specificity are independent of each other when compared across models. Both measures are also independent of prevalence that is the proportion of sites in which the species was recorded as present (Table 2.7 no. 1, McPherson et al. 2004, Allouche et al. 2006). However, it should also be noted that both measures simply reflects how well the model predicts one category (presence or absence) without indicating how many mistakes are made

in the other (McPherson et al. 2004). Chance alone could lead to high sensitivity for particularly prevalent species or high specificity for very rare species (Olden et al. 2002). In contrast, AUC is a robust measure, designed to reflect predictive performance in absence and presence simultaneously (Cicchetti & Feinstein 1990). It juxtaposes correct and incorrect predictions over a range of thresholds (McPherson et al. 2004, Fielding & Bell 1997). Nonetheless, creating a predictive map based on presence/absence of one species requires some probability at which to accept the presence of the target organism (Manel et al. 2001). Final target in conservation ecology is a predictive spatial map on habitat suitability for a respective model species or species' potential occurrence. As conventional threshold a value of 0.5 has been used in ecology (Manel et al. 1999a; 2001, Luck 2002, Stockwell & Peterson 2002, Bailey et al. 2002, Woolf et al. 2002).

The calculation of all ROC plots was performed by R software 2.14.2 (R Development Core Team 2012) applying R packages "PresenceAbsence" (Freeman 2007) and "pROC" (Robin et al. 2011). The number of thresholds was set to 100.

3 Profiles of the distribution and ecological requirements of the macroinvertebrate species in the Upper Ruhr catchment

Parts of this chapter were subject to two graduate theses of Volker Decker and Stina Sauer.

3.1 Introduction

Macroinvertebrate species are a widespread, abundant and highly diverse group of aquatic organisms that includes insects, crustaceans, molluscs, annelids, leeches and flatworms. Benthic macroinvertebrates are large enough to be visible to the naked eye. These species live either on the surface of the river bed or banks or in the sediment (interstitial) and comprise several types of feeding groups e.g. deposit-feeders, filter-feeders, grazers and predators. Thus, they constitute an important link in the aquatic food web between producers (algae, bacteria) and higher consumers such as fish (Woodward & Hildrew 2002), contributing to the flow of energy and nutrients (Covich et al 1999). They inhabit all types of standing and running waters, from fast-flowing mountainous streams to slow-flowing large rivers and estuaries.

Due to their strong response to the surrounding environmental conditions (e.g. instream habitats, water quality) and available resources, macroinvertebrate species have a long history as aquatic bioindicators (Kolkwitz & Marson, 1909). The benthic community but also even single species reflect the overall condition of the aquatic environment. Especially for assessing the water quality in rivers as a function of ecosystem health, macroinvertebrates are used to determine the level of pollution because of their known tolerance, limited mobility, wide range of feeding types and life spans. The large number of species favorably possesses a wide range of responses to stressors such as organic pollutants, sediments, and toxicants. Thus, macroinvertebrate indicators may show effects of cumulative short- and long-term pollution events. Kolkwitz & Marson (1909) firstly developed the idea of saprobity in rivers as a measure of pollution by mainly organic matter and the consequential decrease in dissolved oxygen. The saprobic system has been extended and revised several times since its creation (e.g. Zelinka & Marvan 1961, Sládeček 1965, Armitage et al. 1983, Friedrich 1990, Friedrich & Herbst 2004) and is still established as an inherent part of the standard river assessment system PERLODES in Germany.

Moreover, macroinvertebrates function as indicators for the trophic status of lakes (Brinkhurst 1974), the longitudinal zonation (River Continuum Concept, Vannote et al. (1980) and its extensions) and hydromorphological degradation (Lorenz et al. 2004, Feld 2004) of rivers. Macroinvertebrate distribution is influenced by a variety of hydromorphological variables such as flow conditions (Statzner et al. 1988), substratum characteristics like particle size (Culp et al. 1983), texture (Lamberti & Resh 1979) and heterogeneity (Beisel et al. 2000, Boyero 2003), e.g. content of organic matter or dead wood. Hydromorphological conditions and thus, alterations therefore affect macroinvertebrate assemblages through a variety of individual factors that are mutually dependent. For instance, the composition of instream microhabitats is strongly influenced by channel bed and riparian alteration (Kemp et al. 1999). Dams and impoundments contribute to changing flow conditions and temperature regimes (Ward &

Stanford 1979). The removal of dead wood and debris leads to a loss of several specialist species. Lacking riparian vegetation induces a loss in production rate (Bunn et al. 1999) and changing water temperatures (Sponseller et al. 2001). Related to river morphology, land use appears to be another key factor influencing macroinvertebrate community composition among sites (Sponseller et al. 2001, Allan 2004, Collier 2008, Feld 2012). Urban and industrial land coverage in the riparian zone of a river is correlated to the degraded hydromorphological conditions and may cause significant changes in streams including physical features, conductivity, nutrients, habitat condition, riparian quality and thus macroinvertebrate metrics (Miserendino et al. 2011). Hence, urban land use represents a pressure with the most negative impact on macroinvertebrate indices, while forests were found to have a positive effect (Wasson et al. 2010, Miserendino et al. 2011). In addition, macroinvertebrate water- and habitat quality-related metrics are highly responsive to the percentage of cropland at different spatial scales (Feld 2012). Thus, assessing the direct effects of hydromorphological degradation on the aquatic fauna is challenging because of the presence of other stressors like land use acting simultaneously (Friberg et al. 2009).

Besides benthic diatoms, macrophytes and fish, benthic macroinvertebrates constitute an important organism group used to assess the ecological status of water bodies as required by the European Water Framework Directive (WFD; European Commission 2000). The WFD demands to protect or restore the ‘good ecological status’ of water bodies at all scales. The abundance and ecological traits of invertebrate species were therefore reported and classified in detail (Schmidt-Kloiber & Hering 2012) and are being applied as standard metrics in river assessment throughout Europe, in terms of biodiversity in rivers (Vinson & Hawkins 1998, Ward & Tockner 2001, Feld et al. 2014), success of river restoration (e.g. Lepori et al. 2005, Clements et al. 2010, Palmer et al. 2010, Sundermann et al. 2011a) and climate change effects (Durance & Ormerod 2007, Burgmer et al. 2007, Lawrence et al. 2010, Filipe et al. 2013, Hershkovitz et al. 2015). With respect to the WFD, the German Assessment System PERLODES includes both the Saprobic Index and the German Fauna index (Lorenz et al. 2004) to account for the impact of water quality, riverine hydromorphological degradation and land use on benthic macroinvertebrates and thus, the ecological status of rivers.

With this chapter, I wish to contribute to the knowledge of the species’ ecology and their recent distribution and to give an overview on the species’ relation to broad- and fine-scale environmental conditions. In the following sections the distribution of the model species within the study area, their habitat preferences and their relation to specific environmental variables used for distribution modelling in chapters 4 and 5 are described in detail.

3.2 Materials and Methods

The habitat requirements of the species are described based on environmental data collected during field campaigns in 2010 and 2011 and cross-checked with literature. Variables on land use, physical habitat quality, physico-chemistry and substrates as described in chapter 2.4 were used to describe the species' ecological requirements. Spearman rank correlation coefficients were calculated for each species and environmental variables (land use, physical habitat quality, physic-chemistry and substrates).

The sampling of the species was directly related to the substrates (specified in Table 3.1) they were found on. On each sampling site, the specimen were sampled, preserved and identified separately for each substrate type. Due to their simultaneous presence some substrates could not be sampled separately and thus, were mixed (e.g. dead wood and CPOM). Across 225 sampling sites, this resulted in 768 separate samples which were grouped according to Table 3.1. Substrate preference of each model species was computed as percentage of occurrence per substrate group.

Table 3.1: Mesoscale substrates found at in total 225 sampling sites and number of samples per substrate.

Substrate group	Mesoscale substrates	Number of samples per substrate
Lithal	Psammal Akal Microlithal Mesolithal Macrolithal Megalithal	221
Technolithal	Artificial, head-sized cobbles	33
Riparian roots	Riparian roots	138
Macrophytes	Macrophytes	8
Dead wood	Dead wood	96
Lentic	Lentic areas and pools including small-sized substrates like Argyllal, Pelal, FPOM	128
CPOM	CPOM	58
Mixed samples	Samples of mixed substrates that could not be sampled separately (e.g. CPOM and dead wood)	86
Total		**768**

Actual distribution maps of the species were generated using ArcGIS 10 (ESRI 2011). Boxplots and diagrams were generated using Excel 2010 and the statistical software R version 3.0.2 (R Development Core Team 2013).

3.3 General aspects

Eleven macroinvertebrate species were selected that typically inhabit mountainous rivers and streams in the Ruhr catchment. The selection was based on the species' distribution and prevalence known from former sampling campaigns and survey data (provided by the North Rhine-Westphalia State Agency for Nature, Environment and Consumer Protection, LANUV), positive classification into the German Fauna Index (Lorenz et al. 2004), habitat specificity, sensitivity according to the German Assessment System PERLODES and the species' determinability in the field.

The model species cover different taxonomic groups that build the basis for assessment metrics (EPT), several life cycles, different habitats preferred and various feeding types (Table 3.2). Most species typically inhabit mountainous river stretches dominated by mineral hand-sized cobbles to gravel and sandy substrates. Hence, the species selected are characteristically found in rhithral parts of the study catchment. However, *Calopteryx virgo*, *Gammarus pulex* and *Leuctra geniculata* are also found in lower potamal river sections (see specific species descriptions).

Prevalence ranged between 0 and 50% (based on survey data) with *Gammarus pulex* as the most common species. *Siphlonurus lacustris* was the rarest species due to its preference of lentic areas with organic substrates. For instance, *S. lacustris* was found in small riparian standing waters or puddles arising from agricultural machinery. These rare habitats are mostly omitted by the standard multi-habitat sampling used for monitoring which leads to very low frequencies within survey data. According to my sampling campaigns in 2010 and 2011, *S. lacustris* was found at 23% of all sampling sites due to a habitat-specific sampling method. Overall, species prevalence were similar or higher compared to the initial prevalence out of survey data (Figure 3.1). *H. instabilis* was the most common species (52%) whereas *H. incognita* was only found in 8% of all sampling sites.

A maximum of eight out of eleven model species were found at one single sampling site (Figure 3.2). The most species per site were found in the upper Ruhr and its tributaries and, with a lower number of species per site, in some tributaries of the lower Lenne watershed. There are two areas of lacking colonization: i) the main course of the Lenne which is due to the high level of hydromorphological degradation (including many backwater and residual sections) and ii) the southern tributaries of the Lenne upstream to the Bigge confluence which may be caused by former massive pollution including exposure of heavy metals. In contrast to this, the watersheds near to the Lenne source show a strong increase in species numbers compared to the river sections downstream. Some species, namely *Siphlonurus lacustris*, *Perla marginata*, *Dinocras cephalotes*, *Silo pallipes*, *Hydropsyche dinarica* and *Hydropsyche*

instabilis, seem to have recolonized the formerly highly polluted and acidified Lenne watershed via the upper Ruhr tributaries.

A Spearman correlation analysis showed generally low correlations between the species presence/absence and the environmental variables with coefficients below R = 0.4 (Table 3.3). Most correlations were found for land use variables and physico-chemical variables.

Table 3.2: Selected model species and their ecological preferences according to www.freshwaterecology.info (Schmidt-Kloiber & Hering 2012) and their prevalence throughout the Ruhr catchment based on former sampling campaigns and survey data by the North Rhine-Westphalia State Agency for Nature, Environment and Consumer Protection (LANUV) and their classification of the German Fauna Index in mountainous small and medium-sized rivers (Lorenz et al. 2004, Meier et al. 2006). Additional citations are marked by footnotes.

Model species	Substrate preference	Type of life cycle	Stream zonation preference	Dominant feeding types in the larval stage	Species prevalence (%)		Fauna-index Germany	
					Lenne	Ruhr	River type 5	River type 9
Gammarus pulex	lithal and organic substrates, macrophytes [1]	hololimnic	metarhithral – epipotamal	shredder, gatherer	41.5	48.2	-2	+1
Siphlonurus lacustris	organic substrates (macrophytes, POM) and fine sediments (pelal, psammal, akal, microlithal)	hemimetabolous [3]	epirhithral – metapotamal	gatherer/collector	0.0	0.5	0	+1
Calopteryx virgo	living parts/roots of terrestrial plants [2]	hemimetabolous [4]	metarhithral – epipotamal	predator	2.0	2.0	+2	+1
Leuctra geniculata	psammal, akal, lithal	hemimetabolous [5], univoltine –flexible	hyporhithral – epipotamal	gatherer, grazer, shredder, predator	19.0	27.7	0	+1
Dinocras cephalotes	lithal, macrophytes	hemimetabolous [5], semivoltine	hypocrenal – epipotamal	predator, gatherer	12.9	17.0	+1	+1
Perla marginata	lithal, woody debris	hemimetabolous [5], semivoltine	hypocrenal – metarhithral	predator, gatherer	15.0	20.4	+2	+2
Silo pallipes	lithal	holometabolous [6], univoltine	hypocrenal – metarhithral	grazer, gatherer	12.9	31.9	+1	+1
Silo piceus	lithal	holometabolous [6], univoltine	epirhithral – epipotamal	grazer, gatherer	9.5	22.0	0	+1
Hydropsyche dinarica	lithal, macrophytes, woody debris	holometabolous [6]	epirhithral – hyporhithral	passive filter feeder, predator, grazer	9.5	24.1	+2	+2
Hydropsyche incognita	lithal, macrophytes, woody debris	holometabolous [6]	metarhithral – epipotamal	passive filter feeder, predator, grazer	29.3	14.1	n.a.	n.a.
Hydropsyche instabilis	lithal, macrophytes, woody debris	holometabolous [6], univoltine	epirhithral – hyporhithral	passive filter feeder, predator, grazer	12.2	16.2	+1	+2

1 = Welton (1979); 2 = Heidemann & Seidenbusch (2002); 3 = Studemann et al. (1992); 4 = Stoks & Córdoba-Aguilar (2012); 5 = Stewart & Stark (1993); 6 = Waringer & Graf (1997)

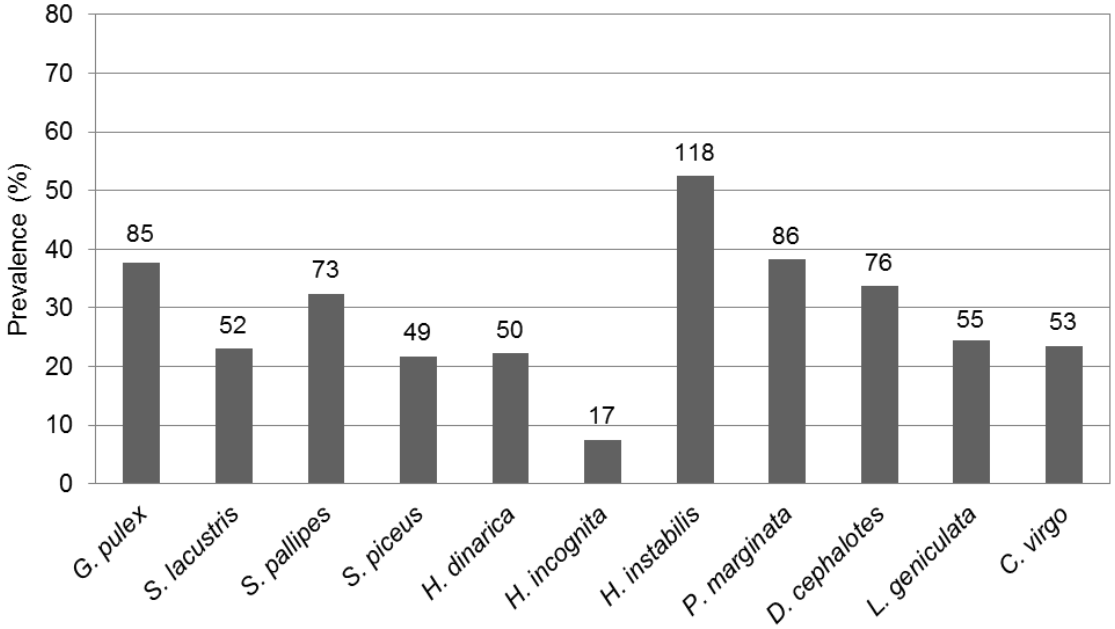

Figure 3.1: Prevalence of macroinvertebrate species across 225 sampling sites in total. The number of occurrence sites is given as numbers above the bar, respectively.

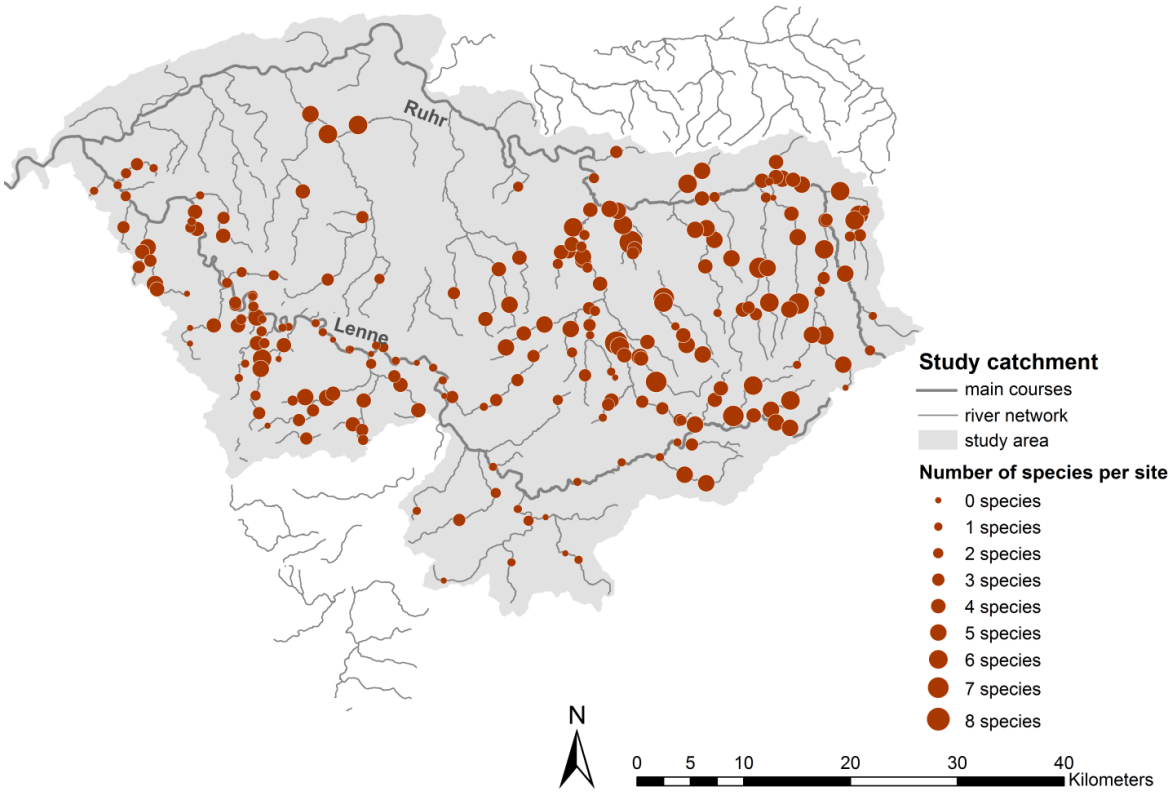

Figure 3.2: Number of model species per sampling site. As a maximum, 8 out of 11 species were found at a single site.

Table 3.3: Spearman rho coefficients of the species' presence/absence and the environmental variables (A = topographical, B = land use, C = physical habitat quality, D = physico-chemistry, E = substrates) using a pairwise deletion. Abbreviations of environmental variables are explained in the tables in chapter 2.4. Coefficients indicating moderate to high correlations (>0.30 and <-0.30) are given in bold. Significant values are given in italics (p<0.05), tested by the rank correlation test in the cor.test() function.

Variable group	Environmental variables	*Gammarus pulex*	*Siphlonurus lacustris*	*Calopteryx virgo*	*Leuctra geniculata*	*Dinocars cephalotes*	*Perla marginata*	*Silo pallipes*	*Silo piceus*	*Hydropsyche dinarica*	*Hydropsyche incognita*	*Hydropsyche instabilis*
A	altitude	*-0.29*	*0.22*	*-0.29*	*-0.23*	*0.26*	*0.24*	***0.47***	-0.03	*0.29*	*-0.16*	*0.28*
	source_m	*0.18*	0.00	***0.31***	***0.36***	***-0.32***	*-0.19*	*-0.18*	*0.22*	*-0.25*	*0.26*	***-0.35***
B	DecFor_n	0.11	*-0.14*	0.06	0.07	0.01	-0.08	*-0.15*	0.00	0.03	0.08	0.00
	ConFor_n	*-0.16*	-0.10	*-0.20*	*-0.23*	*0.29*	*0.23*	0.03	-0.09	***0.30***	*-0.22*	*0.15*
	Ext_n	-0.04	*0.28*	0.04	-0.05	0.06	*0.17*	*0.28*	*0.23*	-0.01	0.03	*0.16*
	Crop_n	0.10	-0.02	0.12	*0.14*	*-0.16*	-0.10	-0.06	0.06	-0.12	*0.20*	-0.04
	Urb_n	*0.15*	-0.05	*0.17*	***0.30***	*-0.19*	*-0.21*	-0.11	0.08	*-0.23*	0.12	*-0.15*
	DecFor_w	0.04	*-0.23*	0.02	0.03	-0.09	*-0.16*	*-0.23*	*-0.18*	0.02	0.04	*-0.13*
	ConFor_w	*-0.15*	*-0.13*	*-0.22*	*-0.26*	***0.35***	*0.29*	0.05	-0.05	***0.30***	*-0.24*	*0.25*
	Ext_w	-0.01	***0.30***	0.06	-0.05	-0.08	0.03	*0.23*	*0.18*	-0.08	0.06	0.04
	Crop_w	*0.16*	0.06	*0.17*	0.10	*-0.19*	-0.10	0.00	0.08	*-0.17*	*0.20*	-0.05
	Urb_w	0.13	-0.07	*0.18*	***0.32***	*-0.27*	*-0.26*	*-0.17*	0.05	*-0.26*	*0.17*	*-0.24*
	F020U200	-0.09	-0.06	*-0.18*	*-0.25*	***0.30***	*0.23*	0.04	*-0.15*	***0.33***	*-0.15*	*0.14*
C	GSG_l	0.07	-0.02	*0.14*	*0.20*	*-0.28*	*-0.28*	0.02	*0.18*	*-0.27*	0.08	*-0.17*
	LocSit	0.09	-0.08	*0.10*	*0.10*	*-0.12*	*-0.21*	*-0.18*	-0.04	*-0.16*	0.07	*-0.16*
	MWD	0.11	-0.12	*0.19*	0.12	*-0.20*	*-0.14*	*-0.26*	0.00	-0.10	*0.18*	*-0.27*
	Planform	0.05	-0.03	*0.13*	*0.18*	*-0.15*	*-0.15*	-0.05	0.10	*-0.24*	*0.14*	-0.12
	Erosion	0.02	-0.13	0.06	*0.15*	*-0.14*	-0.12	*-0.16*	0.00	-0.11	0.08	*-0.22*
	Bars	0.06	0.05	0.04	0.08	-0.05	-0.14	0.07	-0.01	-0.11	-0.04	-0.01
	FeatDyn	-0.06	*-0.16*	-0.05	-0.13	-0.01	-0.11	-0.03	*-0.10*	0.02	-0.01	-0.04
	Riffles	*0.19*	-0.08	-0.01	-0.02	*-0.22*	*-0.26*	-0.02	0.01	*-0.23*	0.00	*-0.20*
	FlowDiv	0.09	*-0.17*	-0.11	-0.11	*-0.20*	*-0.21*	*-0.17*	-0.10	-0.13	-0.05	*-0.19*
	DepVar	0.02	*-0.17*	-0.10	-0.08	-0.10	-0.17	-0.11	0.02	-0.06	0.05	-0.13
	SubsDiv	-0.02	*-0.25*	-0.05	-0.12	-0.12	-0.12	*-0.26*	-0.12	-0.02	0.08	*-0.15*
	FeatChan	-0.09	*-0.21*	-0.02	-0.08	*-0.20*	*-0.19*	*-0.29*	*-0.18*	-0.07	0.08	*-0.17*
	CrSecForm	0.07	-0.11	0.10	*0.24*	-0.08	-0.06	-0.02	0.12	*-0.19*	*0.18*	-0.09
	CrSecDep	0.03	0.08	0.05	*0.24*	0.07	0.11	0.05	*0.15*	0.02	-0.07	0.06
	BankEro	0.04	-0.02	-0.05	*0.21*	-0.01	0.12	0.03	0.12	0.00	-0.03	0.04
	CrSecWid	0.03	*-0.24*	0.10	-0.01	*-0.25*	*-0.20*	*-0.21*	-0.07	*-0.16*	*0.18*	*-0.24*
	RipVeg	*-0.25*	-0.09	-0.01	-0.02	0.03	0.02	-0.10	-0.07	0.05	-0.08	0.00
	BankProt	0.11	-0.08	*0.15*	*0.18*	-0.03	-0.02	-0.06	0.12	*-0.14*	0.11	-0.04
	FeatBank	*-0.13*	-0.02	0.00	-0.01	-0.05	-0.08	0.00	-0.13	0.04	-0.03	-0.04
	Landuse	0.04	*-0.15*	-0.02	0.03	-0.04	-0.05	-0.07	-0.11	-0.05	0.01	0.00
	RipBuff	0.04	0.11	-0.09	0.00	0.02	0.04	0.10	0.12	-0.02	0.06	0.12
	Infrastruc	-0.02	-0.11	0.06	-0.02	-0.09	*-0.13*	*-0.15*	-0.03	0.01	0.00	0.03
D	T_water	0.11	0.02	***0.31***	***0.35***	***-0.32***	*-0.22*	-0.11	0.09	*-0.24*	*0.20*	*-0.23*
	Cond	*0.23*	0.07	*0.19*	0.10	***-0.38***	***-0.30***	*-0.15*	0.07	***-0.34***	0.11	*-0.16*
	O2_cont	-0.10	*0.20*	0.03	-0.04	0.07	0.10	*0.24*	*0.26*	0.12	0.04	0.11
	O2_sat	-0.07	*0.16*	*0.14*	0.13	-0.04	0.04	*0.18*	***0.30***	0.01	0.09	0.01
	pH	0.00	-0.02	*0.21*	*0.25*	*-0.17*	-0.10	-0.03	*0.26*	-0.10	*0.20*	-0.13
	NO3	-0.06	*0.13*	*0.26*	*0.26*	-0.08	0.01	*-0.15*	0.01	-0.10	0.09	-0.09
	NO2	0.09	0.12	*0.29*	***0.33***	***-0.35***	*-0.27*	*-0.14*	0.09	*-0.27*	0.10	*-0.26*
	PO4	-0.01	0.09	0.02	0.10	0.07	0.07	*0.27*	0.03	0.06	0.00	*0.22*
	Chloride	*0.21*	*-0.13*	0.10	0.03	*-0.25*	*-0.24*	*-0.16*	-0.09	*-0.21*	0.07	*-0.23*
	Carb_H	0.13	0.03	*0.28*	***0.35***	*-0.23*	*-0.18*	-0.12	0.12	*-0.19*	0.01	*-0.13*
	Ges_H	*0.21*	*-0.19*	*0.19*	*0.16*	*-0.22*	*-0.17*	*-0.24*	0.02	*-0.17*	0.02	*-0.16*
	Macro	0.03	-0.02	0.12	*0.20*	0.13	0.12	0.08	0.06	0.07	0.10	0.00

Variable group	Environmental variables	*Gammarus pulex*	*Siphlonurus lacustris*	*Calopteryx virgo*	*Leuctra geniculata*	*Dinocars cephalotes*	*Perla marginata*	*Silo pallipes*	*Silo piceus*	*Hydropsyche dinarica*	*Hydropsyche incognita*	*Hydropsyche instabilis*
E	Meso	-0.01	0.02	0.03	*0.20*	*0.16*	*0.17*	0.07	*0.15*	0.05	*0.17*	0.09
	Micro	0.04	0.12	-0.05	*-0.19*	0.01	-0.03	0.08	-0.07	0.05	*-0.14*	*0.16*
	Akal	0.00	*0.15*	0.01	*-0.16*	-0.01	-0.03	0.12	-0.07	-0.03	-0.11	0.13
	PsammPel	0.11	*0.23*	-0.01	0.03	-0.01	0.03	*0.19*	0.12	-0.08	*-0.14*	0.09
	Argyll	*0.22*	0.05	0.04	-0.04	*-0.20*	-0.06	0.09	0.04	*-0.14*	0.03	-0.05
	Tech1	-0.11	*-0.20*	0.07	-0.02	-0.06	-0.07	*-0.15*	0.00	-0.07	-0.07	-0.03
	Algae	*0.24*	0.09	*0.26*	*0.28*	*-0.14*	-0.04	0.05	*0.23*	*-0.19*	0.12	-0.01
	MP	0.03	0.02	-0.04	0.00	*0.17*	*0.17*	*0.23*	0.02	*0.13*	-0.10	*0.15*
	LTTP	*0.13*	*0.14*	*0.16*	0.00	0.04	0.07	*0.14*	0.12	-0.02	0.02	0.09
	Xylal	0.07	0.05	*-0.15*	0.03	0.12	0.10	*0.17*	0.11	0.08	-0.08	0.12
	CPOM	*0.15*	0.10	0.02	-0.01	*0.14*	0.04	*0.24*	0.11	0.08	-0.01	*0.20*
	FPOM	0.01	*0.24*	*0.22*	0.13	*-0.22*	-0.13	-0.03	*0.19*	*-0.19*	0.05	*-0.18*

3.4 Crustacea, Amphipoda: Gammarus pulex (LINNAEUS, 1758)

Figure 3.3: *Gammarus pulex* (Linnaeus 1758), photo: UDE, Dept. Aquatic Ecology.

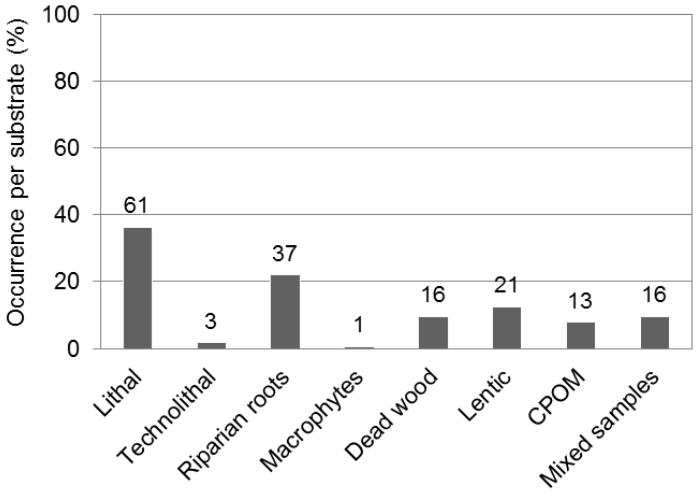

Figure 3.4: Substrate preference of *G. pulex* (%) based on the field campaigns 2010 and 2011 (the number of occurrence sites = 168). The number of occurrence sites per substrate is given as numbers above the bar, respectively.

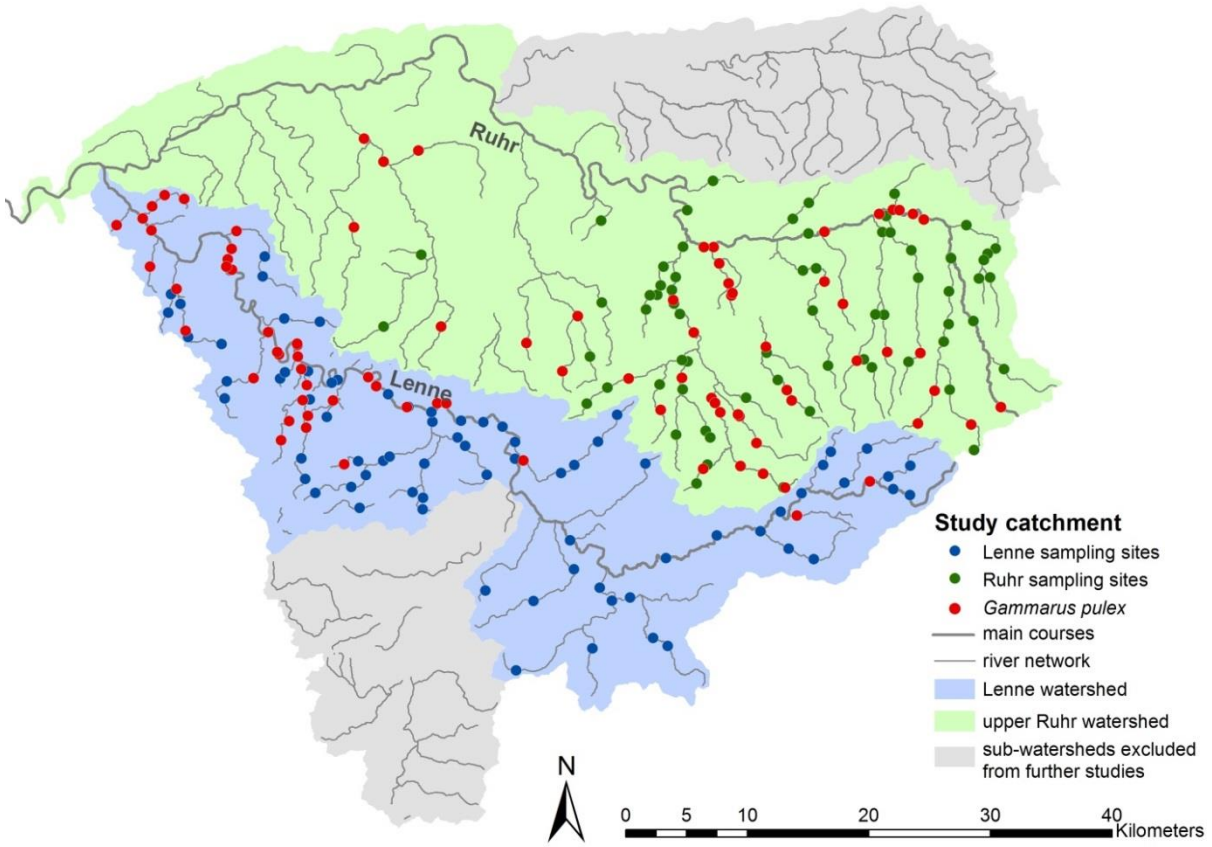

Figure 3.5: Occurrence sites of *G. pulex* in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *G. pulex* was recorded present are given in red.

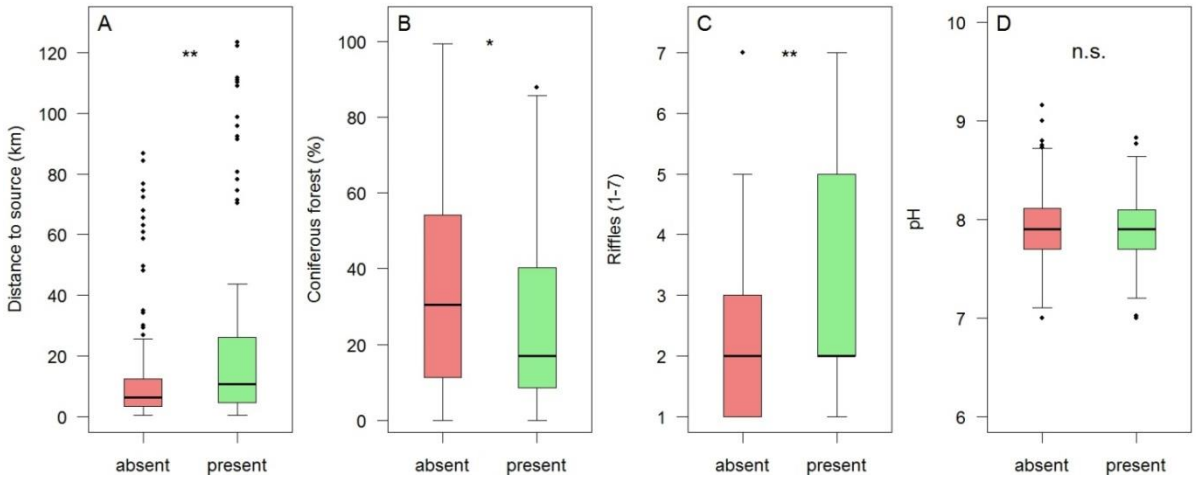

Figure 3.6: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *G. pulex*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Physical habitat quality variables are given in categories ranging from classifications 1 (no alteration) to 7 (complete alteration). Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

Gammarus pulex (Linnaeus 1758) is a hololimnic amphipod species (Crustacea) that is one of the most frequent species within the study area (Table 3.1, Figure 3.1). It mainly occurs in rhithral stream zones and only partly in potamal stream sections (Eder et al. 1995). *G. pulex* prefers a wide range of substrates, occurring on stony as well as organic substrates (CPOM, FPOM, xylal) and macrophytes (Schmedtje & Colling 1996). During my field campaigns, *G. pulex* was also found on lentic areas as well as organic substrates (roots, CPOM, dead wood) to a similar extent (Figure 3.4). Coherent to its dominant feeding type as shredder and gatherer (Eder et al. 1995) this species plays an important role in decomposition of organic substances in mountainous areas (Holm 1989). Elliott (2005) describes *G. pulex* as an omnivore feeder on plant and animal debris (e.g. macroinvertebrates and fish). *G. pulex* is distributed across the entire study catchment except the upper Lenne watershed (Figure 3.5). This finding is coherent with former studies and may be due to more acidic conditions in that area caused by higher shares of riparian coniferous forest or local heavy metal pollution (Ruhrverband 2013). According to my data base, *G. pulex* was found in river sections with percentages of coniferous forest up to 40% (Figure 3.6B), but a significant correlation between its occurrence and pH could not be found (Figure 3.6D).

3.5 Ephemeroptera, Siphlonuridae: Siphlonurus lacustris (EATON, 1870)

Figure 3.7: Larvae of *Siphlonurus lacustris* (Eaton 1870), photo: UDE, Dept. Aquatic Ecology.

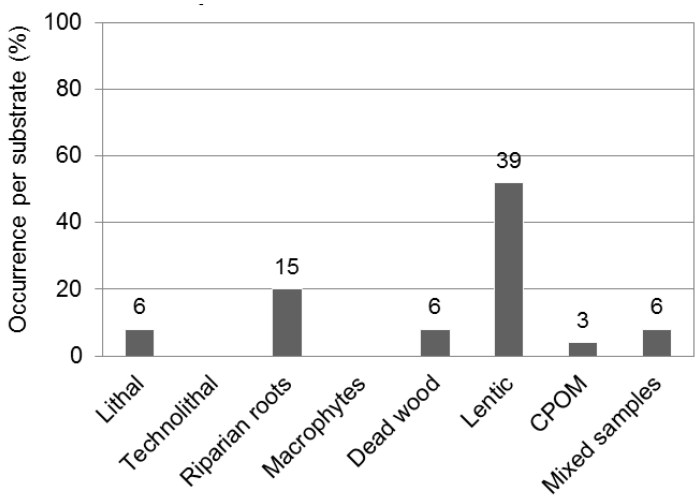

Figure 3.8: Substrate preference of *S. lacustris* (%) based on the field campaigns 2010 and 2011 (the number of occurrence sites = 75). The number of occurrence sites per substrate is given as numbers above the bar, respectively.

Siphlonurus lacustris (Eaton 1870) is the only selected species that mainly occurs in standing waters in littoral stream sections and even temporary small water bodies in the riparian zone (e.g. small puddles or tracks of agricultural vehicles). This species is limnophilic and thus, it is rarely found in slowly flowing streams (Schmedtje & Colling 1996, Buffagni et al. 2009). Hence, *S. lacustris* prefers organic (e.g. roots, CPOM, dead wood) and fine-sediment substrates (Belfiore 1983), particular organic matter (POM, Figure 3.8, Figure 3.10C) and sandy to muddy sediments with fine detritus where it feeds as gatherer and collector (Elliott et al. 1988, Bauernfeind et al. 2002). Although found in standing waters, oxygen saturation was significantly higher at occurrence sites of *S. lacustris*. Its initial prevalence based on survey data was very low (Table 3.2) due to the standardized sampling method (Multi-Habitat-Sampling) that often ignores special substrates and small riparian water bodies. Despite of this fact, *S. lacustris* is known to occur in the study area (Daniel Hering, personal communication) and was found mainly in small streams in the Upper Ruhr watershed, dominated by extensive land use, e.g. grassland (Figure 3.9, Figure 3.10B). According to the Red List of North Rhine-Westphalia, *S. lacustris* is listed in the pre-warning list (V) indicated as rarely abundant (LANUV 2011, Haybach & Eiseler 2011).

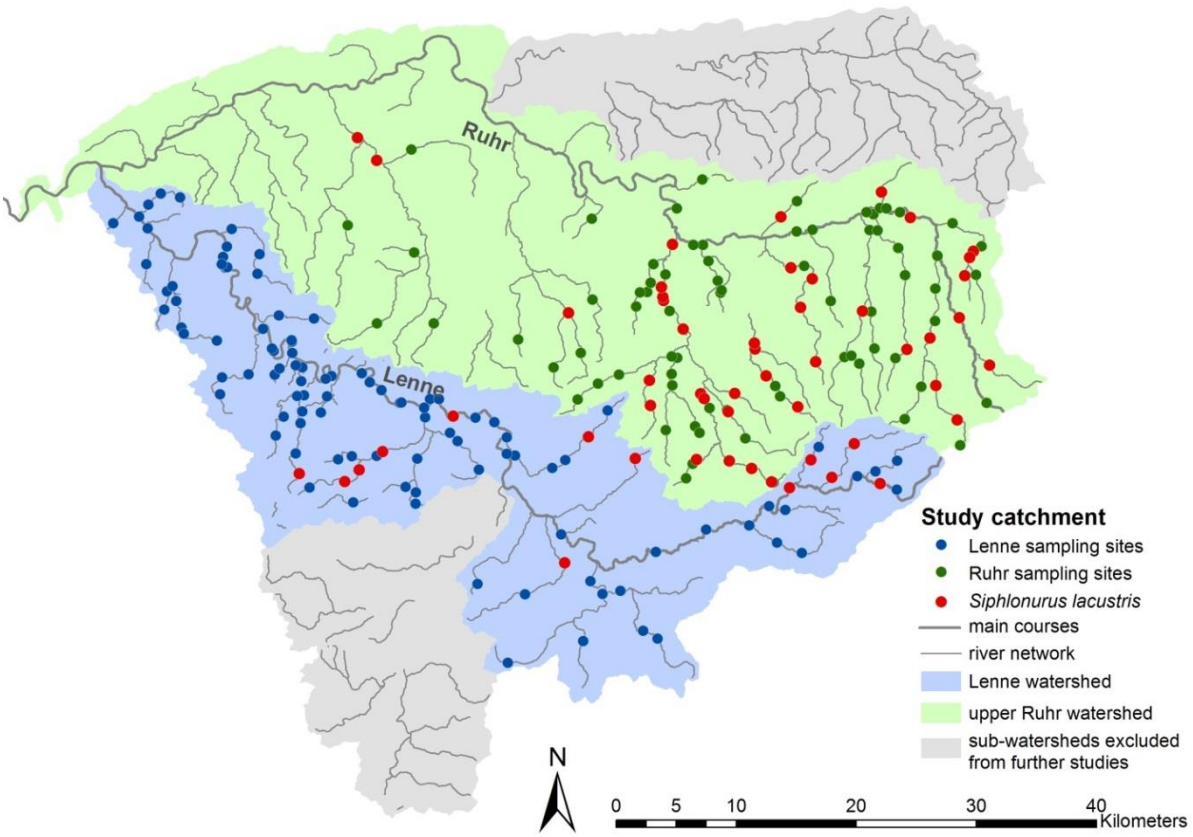

Figure 3.9: Occurrence sites of *S. lacustris* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *S. lacustris* was recorded present are given in red.

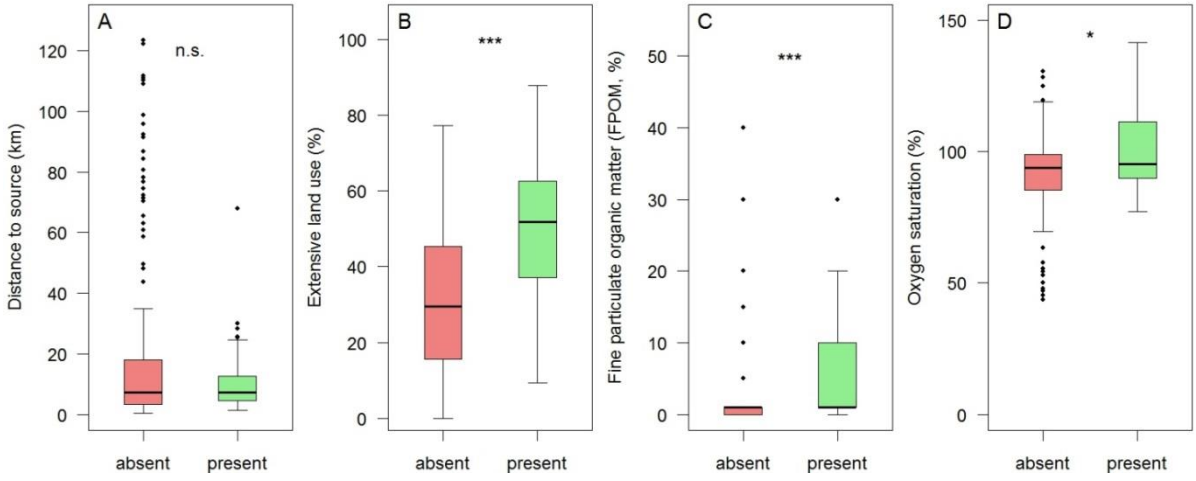

Figure 3.10: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *S. lacustris*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

3.6 *Odonata, Calopteryigidae: Calopteryx virgo (LINNAEUS, 1758)*

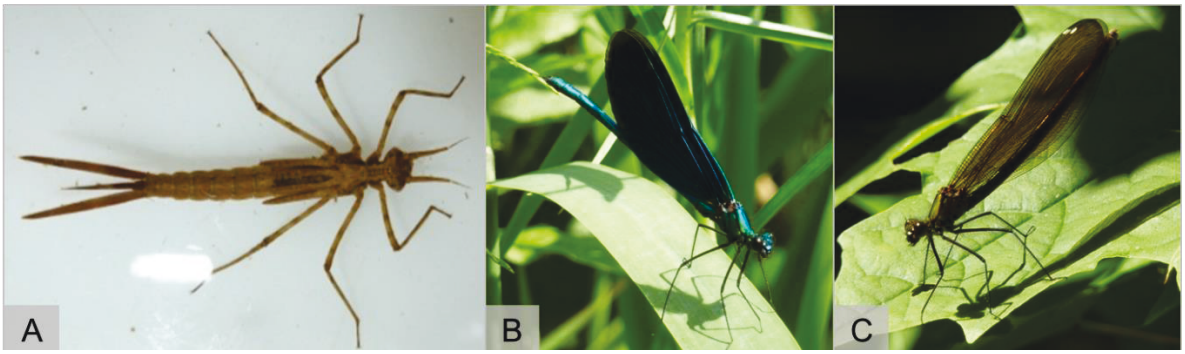

Figure 3.11: (A) larvae of *Calopteryx virgo* (Linnaeus 1758), (B) adult male of *C. virgo*, (C) adult female of *Calopteryx* sp.

Calopteryx virgo (Linnaeus 1758) is a zygopteran dragonfly which is highly sensitive to pollution and hydromorphological degradation in rivers. *C. virgo* prefers meta- to epipotamal stream sections (Janecek et al. 1995) and occurs in rivers with high current velocity and high oxygen saturation (rheophil, Figure 3.14D), but may also be found in lakes (Heidemann & Seidenbusch 2002). According to my data set, *C. virgo* was prevalent in 53 out of 225 sampling sites (24%). According to the Red List of North Rhine-Westphalia, *C. virgo* is listed in the pre-warning list (V) (LANUV 2011).

The optimal temperature is on average 13-18°C (Schorr 1990, Schmedtje & Kohmann 1992, Heidemann & Seidenbusch 2002). *C. virgo* was mostly found in stream sections with higher water temperatures (12-15°C, Figure 3.14C) that is coherent with its occurrence in sections up to 30 km in distance to source (Figure 3.14A). *C. virgo* was found in rhithral as well as potamal sections within the study area (Figure 3.13). Longer periods of water temperatures higher than 22°C may act lethal to larval stages (Sternberg & Buchwald 1999). *C. virgo* can be found in streams with partly sunny, partly shaded river banks with high amounts of riparian vegetation (Heidemann & Seidenbusch 2002). Nevertheless, the species avoids river stretches running through densely forested areas or streams whose banks are densely covered by riparian vegetation (Maibach & Meier 1987). The occurrence of *C. virgo* was significantly related to sections with coniferous forest less than 30% (Figure 3.14B). The larvae inhabit living parts and roots of terrestrial plants that immerse into the water body near to the river bank (Figure 3.12), but can also be found on sandy substrates and gravel (Schmedtje & Kohmann 1992). Larvae are perennial (1-2 years) and feed as predators. They are sensitive to oxygen deficiency in running waters and thus, minimum oxygen content is 6 mg/l (Sternberg & Buchwald 1999).

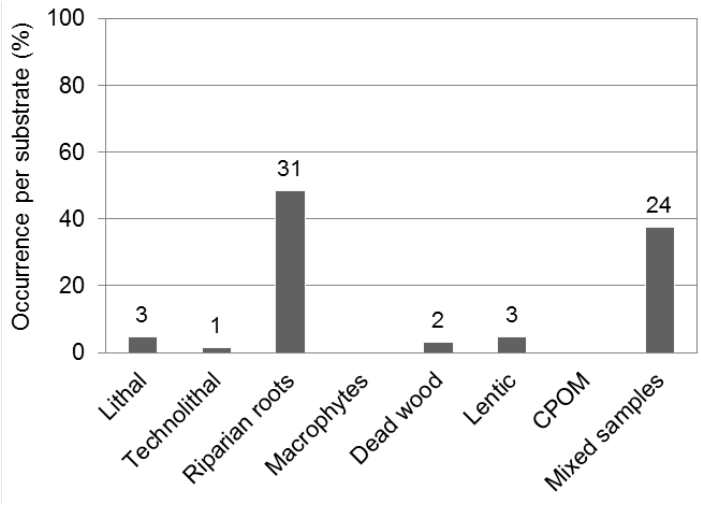

Figure 3.12: Substrate preference of *C. virgo* (%) based on the field campaigns 2010 and 2011 (the number of occurrence sites = 64). The number of occurrence sites per substrate is given as numbers above the bar, respectively.

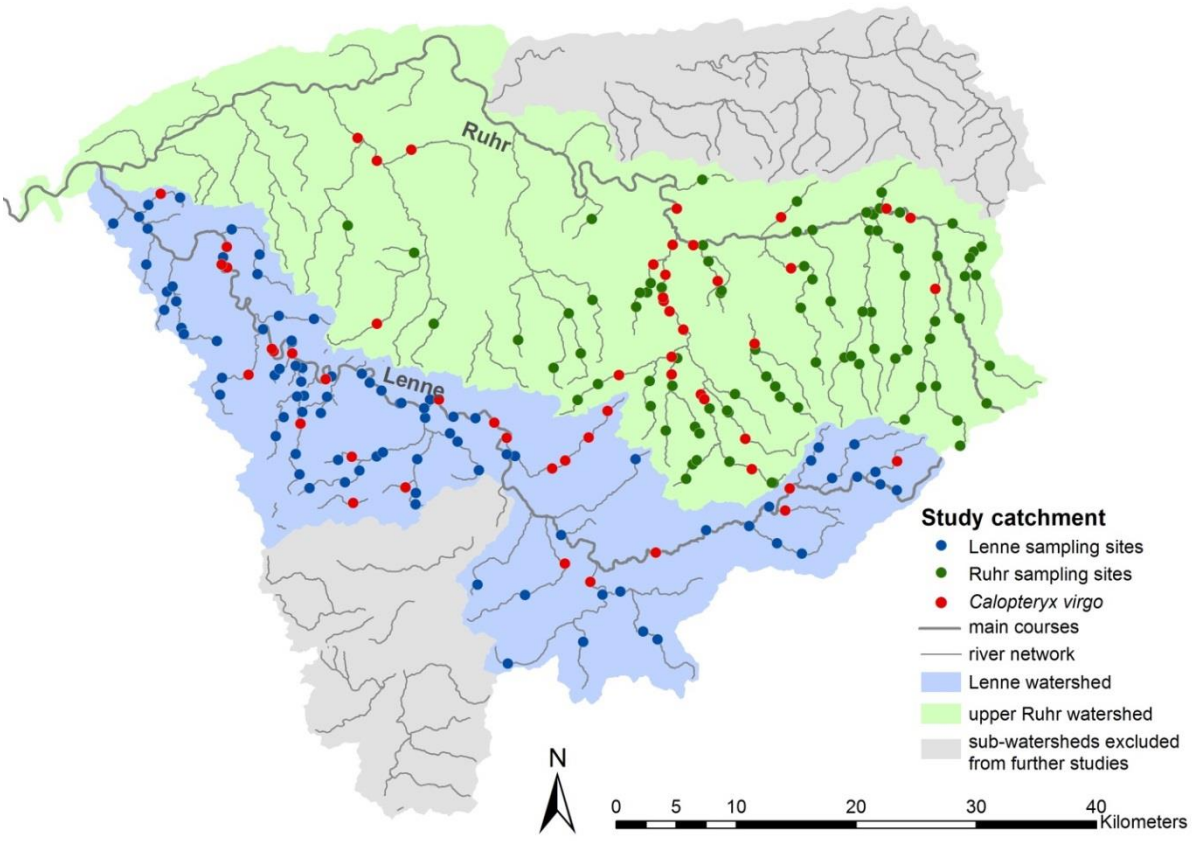

Figure 3.13: Occurrence sites of *C. virgo* in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *C. virgo* was recorded present are given in red.

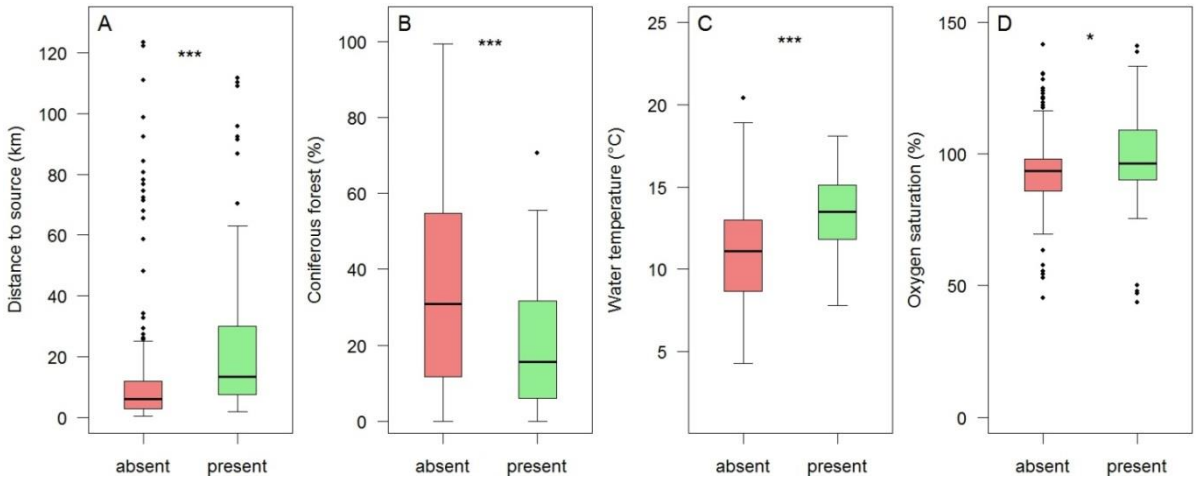

Figure 3.14: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *C. virgo*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

3.7 Plecoptera, Leuctridae: Leuctra geniculata (STEPHENS, 1836)

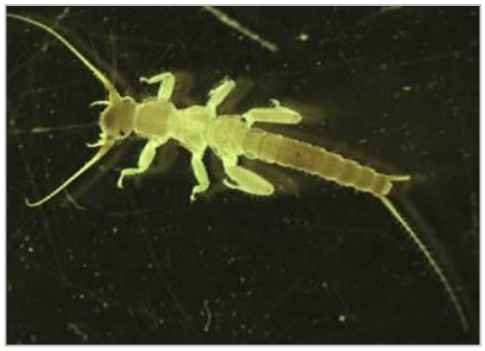

Figure 3.15: Larvae of *Leuctra geniculata* (Stephens, 1836).

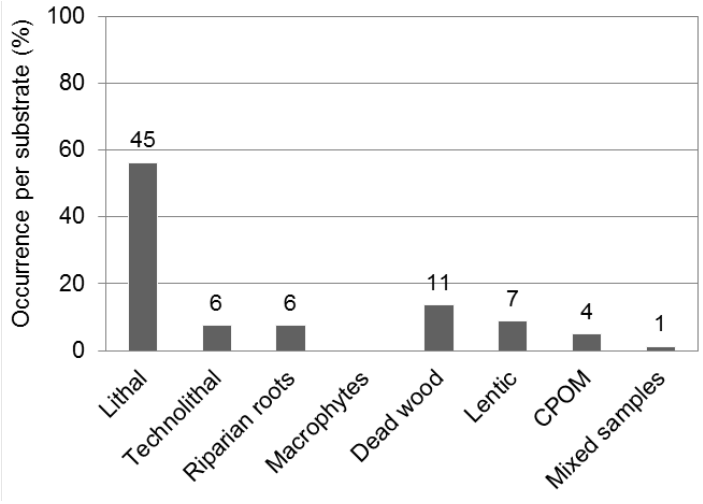

Figure 3.16: Substrate preference of *L. geniculata* (%) based on the field campaigns 2010 and 2011 (the number of occurrence sites = 80). The number of occurrence sites per substrate is given as numbers above the bar, respectively.

Leuctra geniculata (Stephens, 1836) is a small plecopteran species whose larvae are easy to identify due to their characteristic appendices at the proximal antennae (Eiseler & Enting 2010). *L. geniculata* prefers mountainous streams, but also occurs in lowland streams (Eiseler & Enting 2010). While the population was declining during the 1970's (Caspers & Stiers 1977), *L. geniculata* is nowadays found more often occurring in different river types (Eiseler & Enting 2010). *L. geniculata* is therefore in the process of migration into the Ruhr watershed (Armin Lorenz, personal communication), which can be considered as a remigration of a former native species due to the improved river quality and hydromorphology (Eiseler & Enting 2010). Surprisingly, *L. geniculata* was found to show a very patchy distribution within the upper Ruhr watershed (Figure 3.17).

Most of the inhabited river stretches consist predominantly of cobble-gravel-sand substrates and, in some cases *L. geniculata* inhabits fine deposits near the river bank (Pařil et al 2008). Concordant to this, *L. geniculata* was also found on various organic substrates like roots, dead wood and CPOM as well as in lentic areas with sandy to fine-particulate substratum (Figure 3.16). According to Graf et al. (2002b), the *Leuctra* larvae are very probably detritivorous shredders and grazers with a higher preference for algae. *L. geniculata* belongs to late summer–autumn species emerging from August till November (Despax 1951, Kis 1974, Elliott 1987, Sánchez-Ortega et al. 2002, Eiseler & Enting 2010). The species prefers neutral or slightly alkaline waters with pH ranging 7.0 to 9.0 (Pařil et al. 2008). Furthermore, the species

was also found in watercourses with lower water quality, higher shares of urban areas and settlements within the riparian zone and higher water temperatures up to 15°C (Figure 3.18).

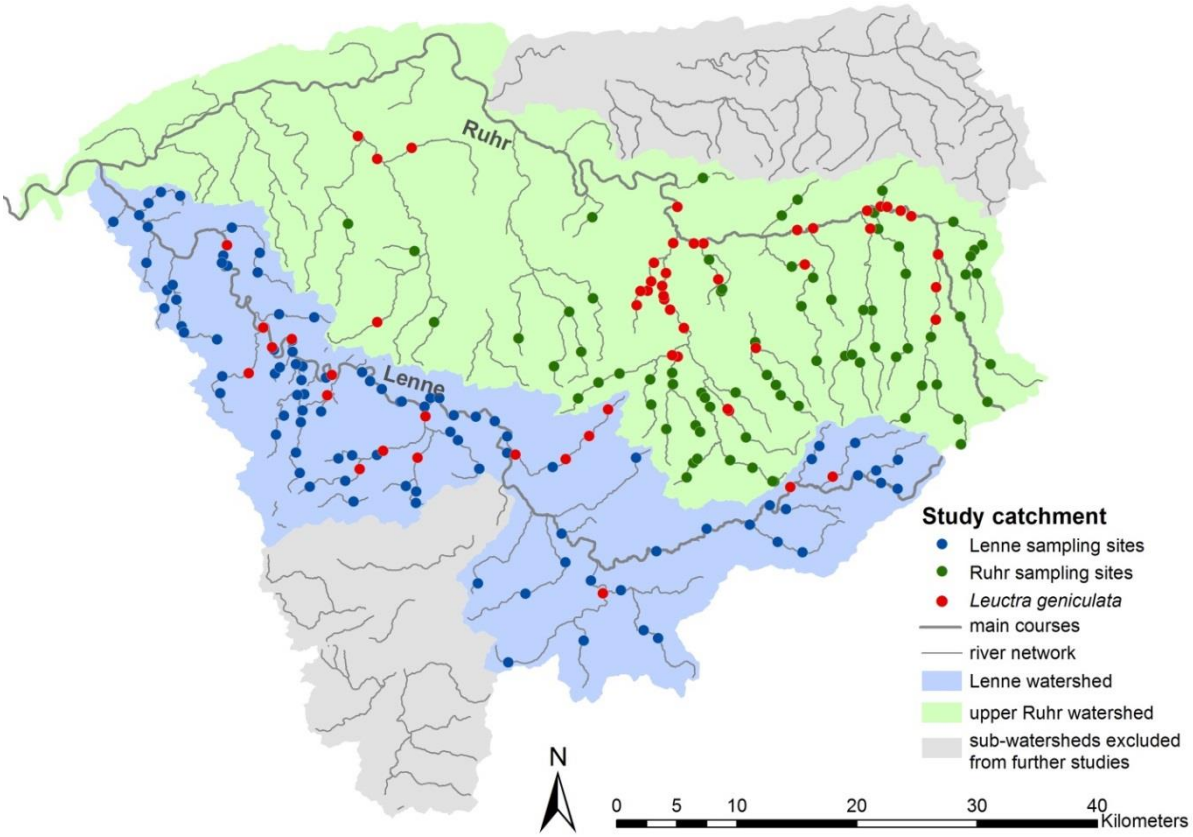

Figure 3.17: Occurrence sites of *L. geniculata* in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *L. geniculata* was recorded present are given in red.

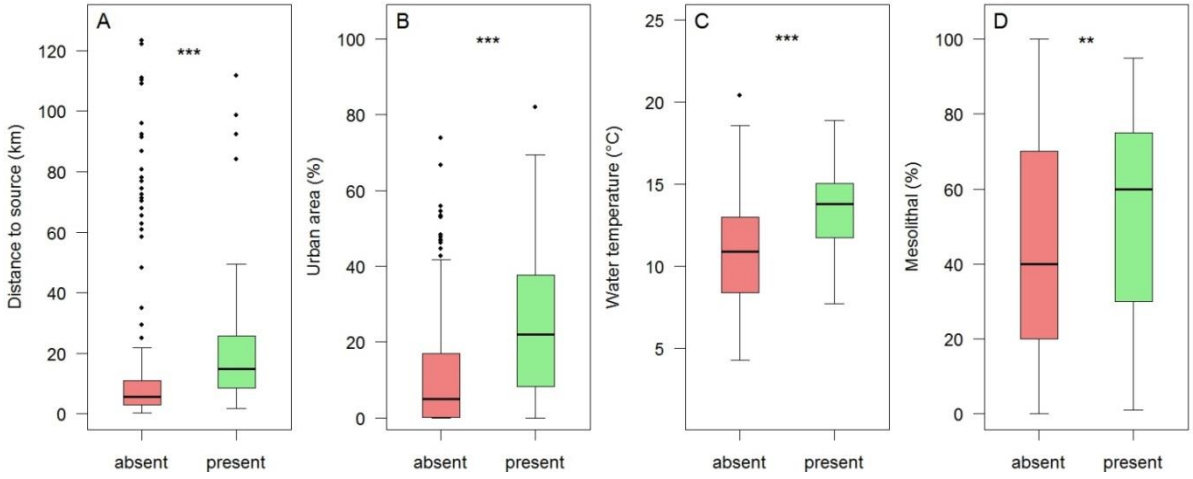

Figure 3.18: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *L. geniculata*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

3.8 Plecoptera, Perlidae: Perla marginata (PANZER, 1799) and Dinocras cephalotes (CURTIS, 1827)

Figure 3.19: Larvae of *Perla marginata* (PANZER, 1799), photo: Eiseler & Enting 2010, Verbreitungsatlas der Steinfliegen (Plecoptera) in Nordrhein-Westfalen.

Figure 3.20: Larvae of *Dinocras cephalotes* (CURTIS, 1827), photo: Eiseler & Enting 2010, Verbreitungsatlas der Steinfliegen (Plecoptera) in Nordrhein-Westfalen.

Perla marginata (Panzer, 1799) and *Dinocras cephalotes* (Curtis 1827) are large Perlidae species typically inhabiting mountainous, fast flowing rhithral stream sections with stony and pebble substrates. These species are indicators of good water quality. Schmedtje & Colling (1996) classified *P. marginata* as inhabitant of epi- to metarhithral parts of rivers. *Dinocras cephalotes* shows a large overlap with *P. marginata* in stream zonation preference occurring in epi- to metarhithral but also closer to the source in very small mountainous rivers (Schmedtje & Colling 1996, Figure 3.22 and Figure 3.24), but this was not evident according to my data (Figure 3.23A and Figure 3.25A). Sánchez-Ortega et al. (2002) updated this distribution pattern to stronger preference to meta-, hyporhithral and epipotamal. As stated by Haidekker & Hering (2007) and Valladolid et al. (2007), both species tolerate a broad range of temperature (0-20°C), but are generally found at temperatures less than 14°C (Rolauffs 2006, Pottgiesser & Sommerhäuser 2008). Both species prefer stony and pebble substrates (Graf et al. 2009). *D. cephalotes* additionally occurs on macrophytes (Graf et al. 2009, Schmedtje & Colling 1996) as well as other organic substrata like roots, dead wood, CPOM and artificial stony substrates (Figure 3.21B), whereas *P. marginata* also prefers woody debris (Graf et al. 2009). The presence of both species is negatively affected by urban areas within the riparian zone (Figure 3.23B and Figure 3.25C) and conductivity higher than approx. 400 µS/cm (Figure 3.23D and Figure 3.25D).

The larvae are easily identifiable by their body size (up to 40 mm), a long pair of antennae, two long cerci and visible filament gills between the thoracal legs. *P. marginata* has characteristic head markings and can be recognized by lack of anal gills. *D. cephalotes* is darker in its body

colour without pale longitudinal bands on abdomen (Zwick 2004). Both larvae mainly feed on other insect larvae. Besides this, larvae also feed as gatherers and collectors of detritus and algae.

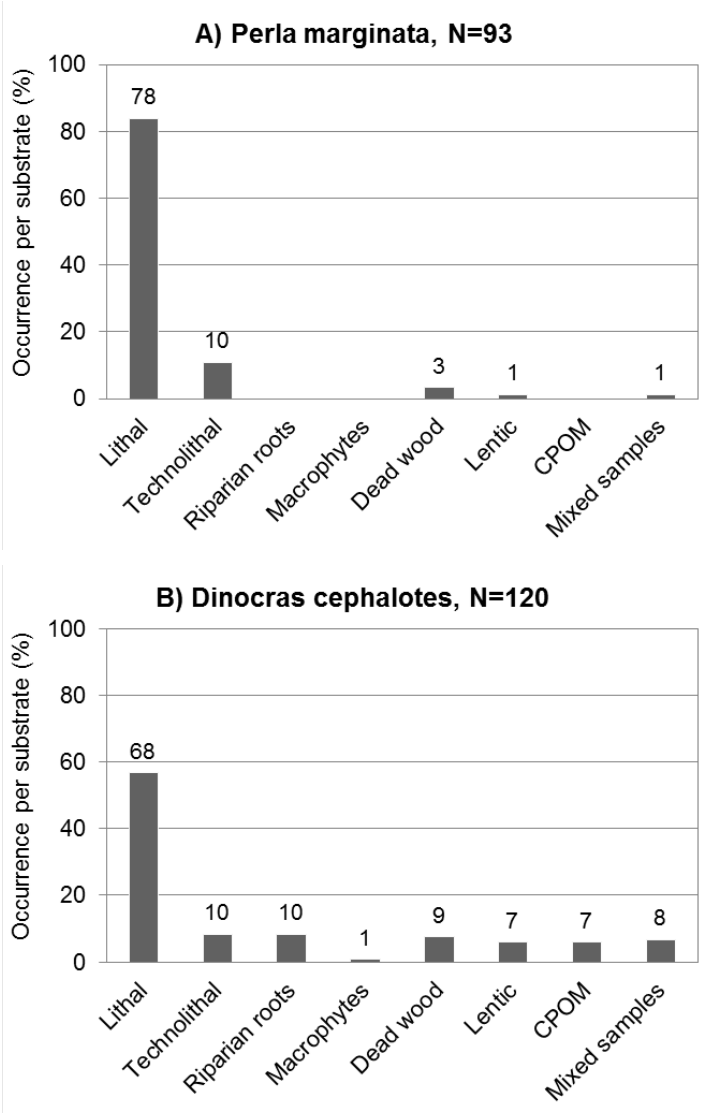

Figure 3.21: Substrate preference of the two Perlidae species (%) based on the field campaigns 2010 and 2011. The total number of occurrence sites is given as N. The number of occurrence sites per substrate is given as numbers above the bar, respectively.

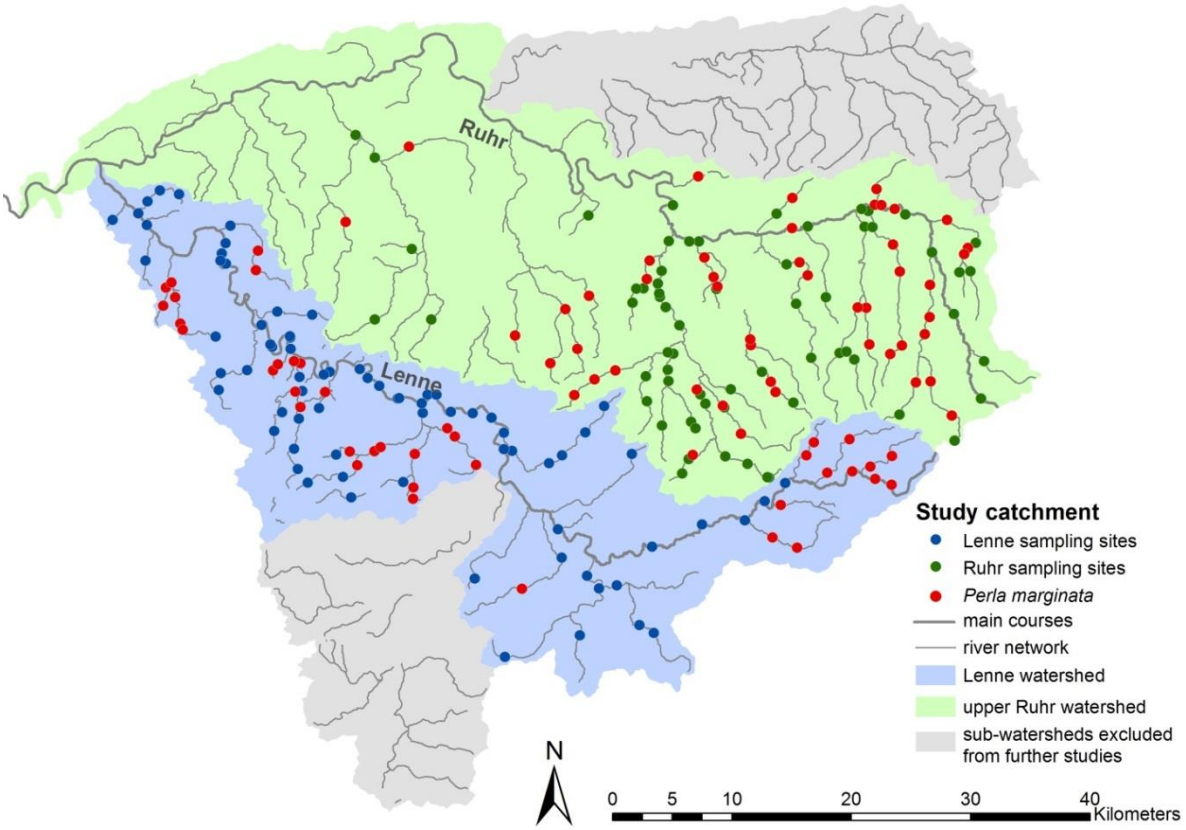

Figure 3.22: Occurrence sites of *P. marginata* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *P. marginata* was recorded present are given in red.

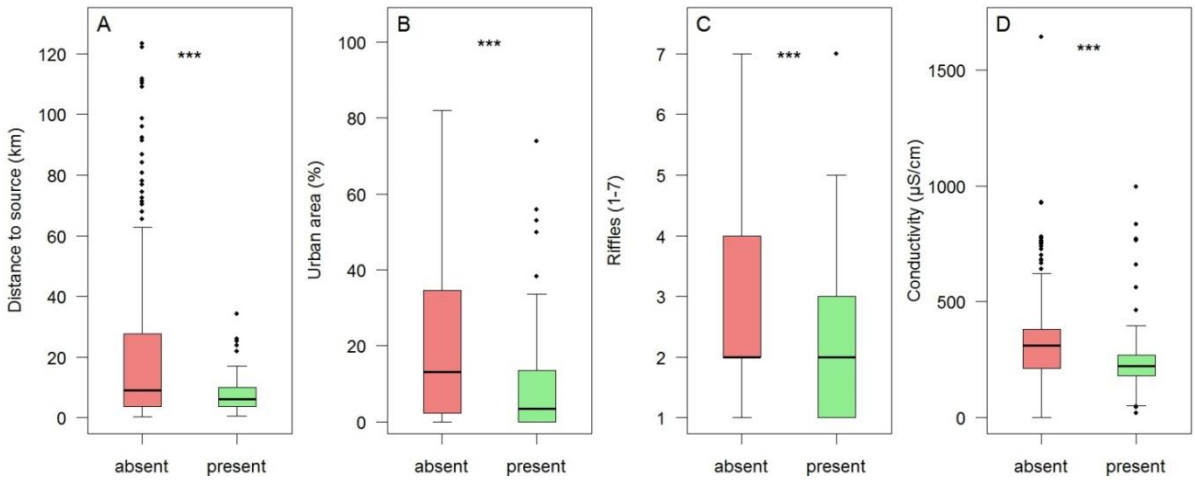

Figure 3.23: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *P. marginata*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Physical habitat quality variables are given in categories ranging from classifications 1 (no alteration) to 7 (complete alteration). Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

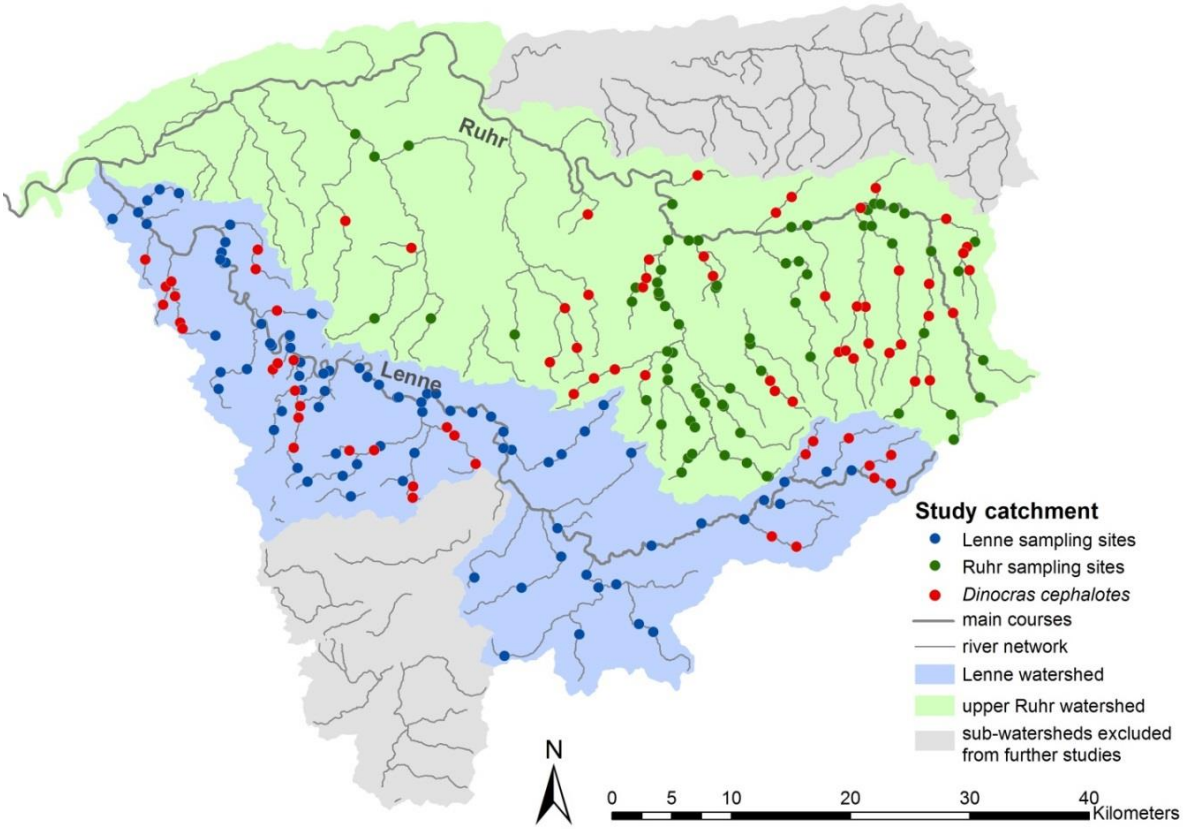

Figure 3.24: Occurrence sites of *D. cephalotes* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *D. cephalotes* was recorded present are given in red.

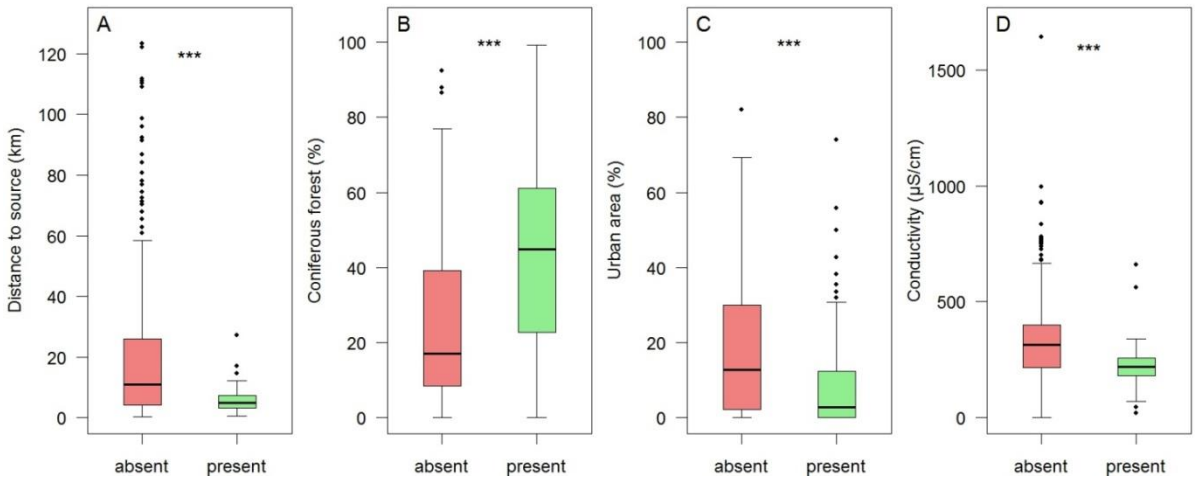

Figure 3.25: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *D. cephalotes*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

3.9 *Trichoptera, Goeridae: Silo pallipes (FABRICIUS, 1781) and Silo piceus (BRAUER, 1857)*

Figure 3.26: Larvae of *Silo pallipes* (Fabricius 1781).

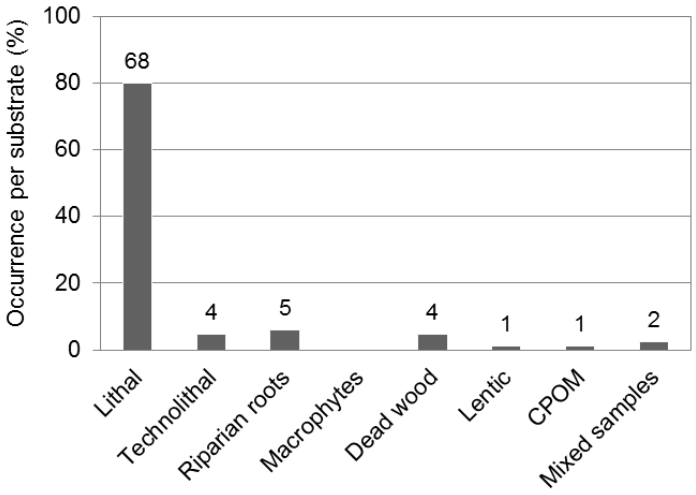

Figure 3.27: Substrate preference of *S. pallipes* (%) based on the field campaigns 2010 and 2011 (the number of occurrence sites = 85). The number of occurrence sites per substrate is given as numbers above the bar, respectively.

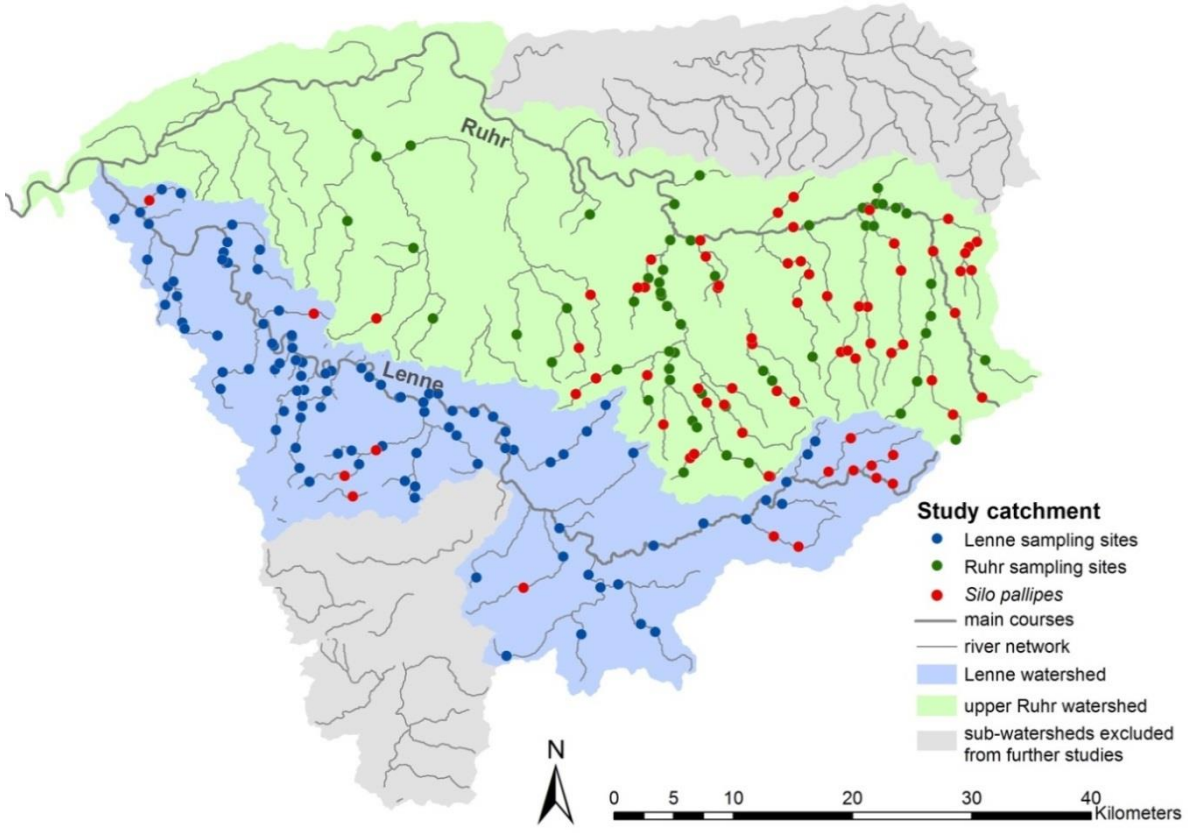

Figure 3.28: Occurrence sites of *S. pallipes* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *S. pallipes* was recorded present are given in red.

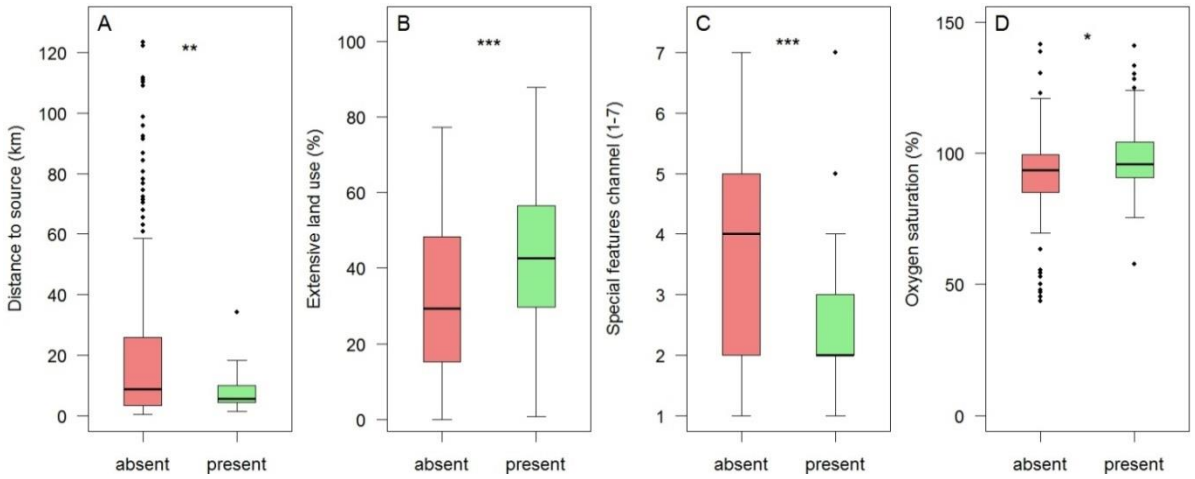

Figure 3.29: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *S. pallipes*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Physical habitat quality variables are given in categories ranging from classifications 1 (no alteration) to 7 (complete alteration). Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

Silo pallipes (Fabricius 1781) and *Silo piceus* (Brauer 1857) are rheophilic species belonging to the family Goeridae with a large overlap in their ecological preferences. Both species mainly inhabit rhithral zones of mountainous streams with high oxygen contents (Holm 1989, Burmeister 1992, Figure 3.29D and Figure 3.31D, >10 mg/l). *S. piceus* also occurs in lower parts (epipotamal), whereas *S. pallipes* can also be found in crenal parts with higher oxygen content (Graf et al. 2002a). Both species were found mainly in the Upper Ruhr watershed in small near-natural stream sections (Figure 3.28 and Figure 3.31, Figure 3.29A and Figure 3.32A) on preferably stony substrates (Figure 3.27 and Figure 3.30) with higher shares of extensive land use and higher amounts of special features within the channel, e.g. scour- and backwater pools, rapids, cascades (Figure 3.29B+C and Figure 3.32B+C). Extensive land use causes less pollution and alteration than urban areas or cropland and hence, may be more preferred than other land coverage classes. The lack of negative effects of urban areas and cropland may therefore indirectly caused by the distribution restricted to small streams where settlements and agriculture are less common. *S. pallipes* was more common in the study catchment (prevalence 34%) than *S. piceus* (prevalence 22%). Both species prefer gravel and sandy (Kohl 1994, Sauer 1988) as well as micro- and macrolithal substrates (Graf et al. 2008, Figure 3.27 and Figure 3.30) on which they feed as grazers and seldom as sediment feeders (Graf et al. 2002a). This is supported by the positive correlation between coverage of algae and the occurrence of *S. piceus*, for instance (Table 3.3). Goerid larvae are easy to identify in the field because of the characteristic stony dwellings which consists of larger rock fragments at the lateral sides.

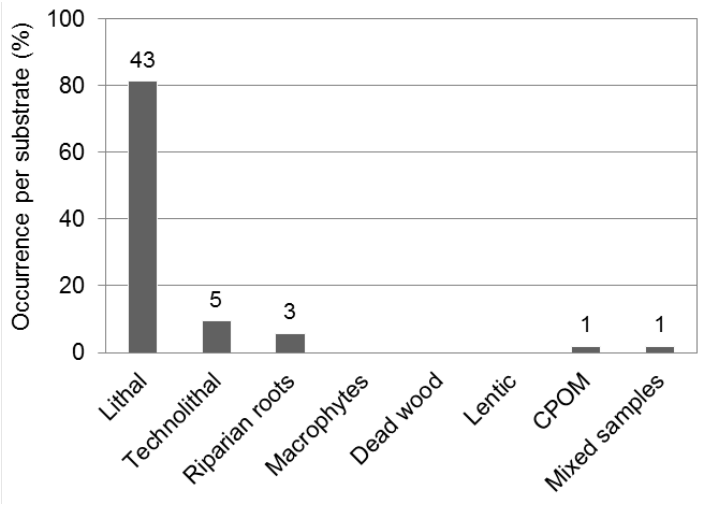

Figure 3.30: Substrate preference of *S. piceus* (%) based on the field campaigns 2010 and 2011 (the number of occurrence sites = 53). The number of occurrence sites per substrate is given as numbers above the bar, respectively.

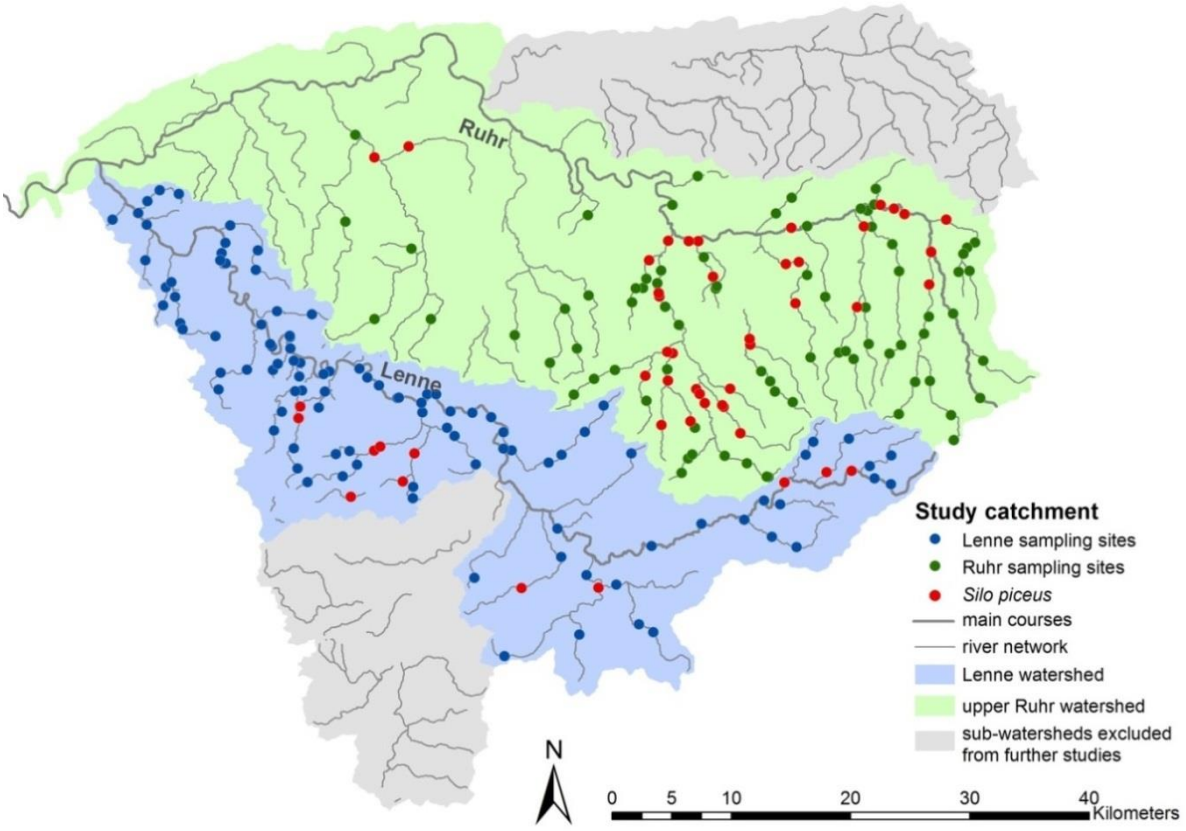

Figure 3.31: Occurrence sites of *S. piceus* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *S. piceus* was recorded present are given in red.

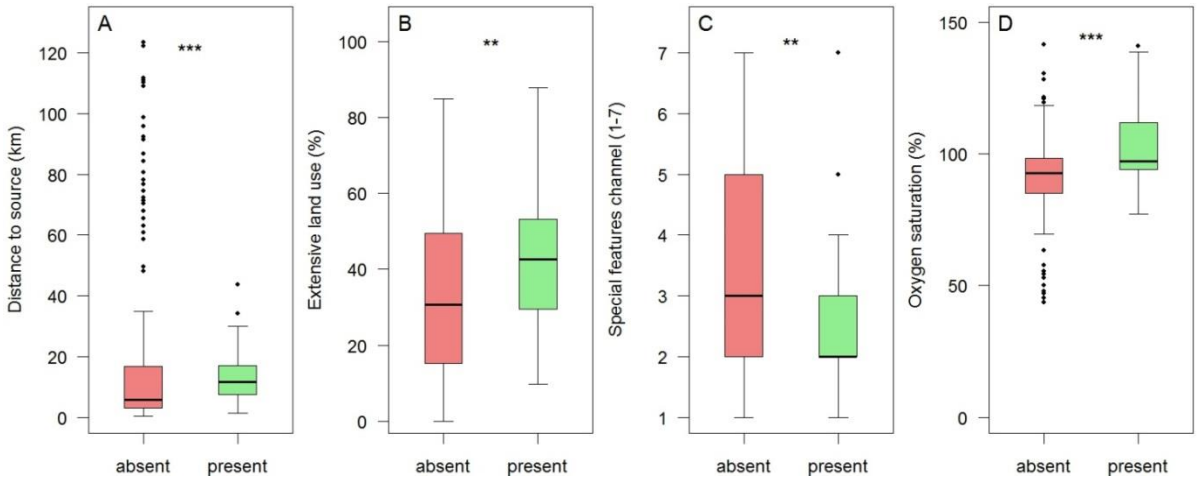

Figure 3.32: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *S. piceus*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Physical habitat quality variables are given in categories ranging from classifications 1 (no alteration) to 7 (complete alteration). Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

3.10 Trichoptera, Hydropsychidae: Hydropsyche dinarica MARINKOVIC, 1979, Hydropsyche incognita PITSCH, 1993 and Hydropsyche instabilis (CURTIS, 1834)

Figure 3.33: Larvae of *Hydropsyche* sp., taxonomic details are visible only via binocular, photo: UDE, Dept. Aquatic Ecology.

The three Hydropsychidae species are indicated to be highly sensitive to hydromorphological degradation (positive classification of the German Fauna Index): *Hydropsyche dinarica* (Marinkovic 1979), *Hydropsyche incognita* (Pitsch 1993) and *Hydropsyche instabilis* (Curtis 1834). These hydropsychids are typical inhabitants of mountainous, fast-flowing and oxygen-rich streams. Larvae can be easily identified by their large, curved bodies, their sclerotized head and thorax and their branched gills along the ventral abdomen. Hydropsychidae Gen. sp. do not construct mobile stony or wooden dwellings but retreats that are fixed to sides of stones and typically composed of collected rock or plant fragments. All three species mainly feed as passive filter feeders by spinning nets to catch algae, detritus and smaller macroinvertebrates. This is why they are also classified as predators and grazers (Graf et al. 2002a). Studies of Schuhmacher & Schremmer (1970) and Schröder (1985) showed that early larval stages of *H. instabilis* feed as grazer and gatherer on stony substrates and only later larval stages spin nets to feed as filter feeder.

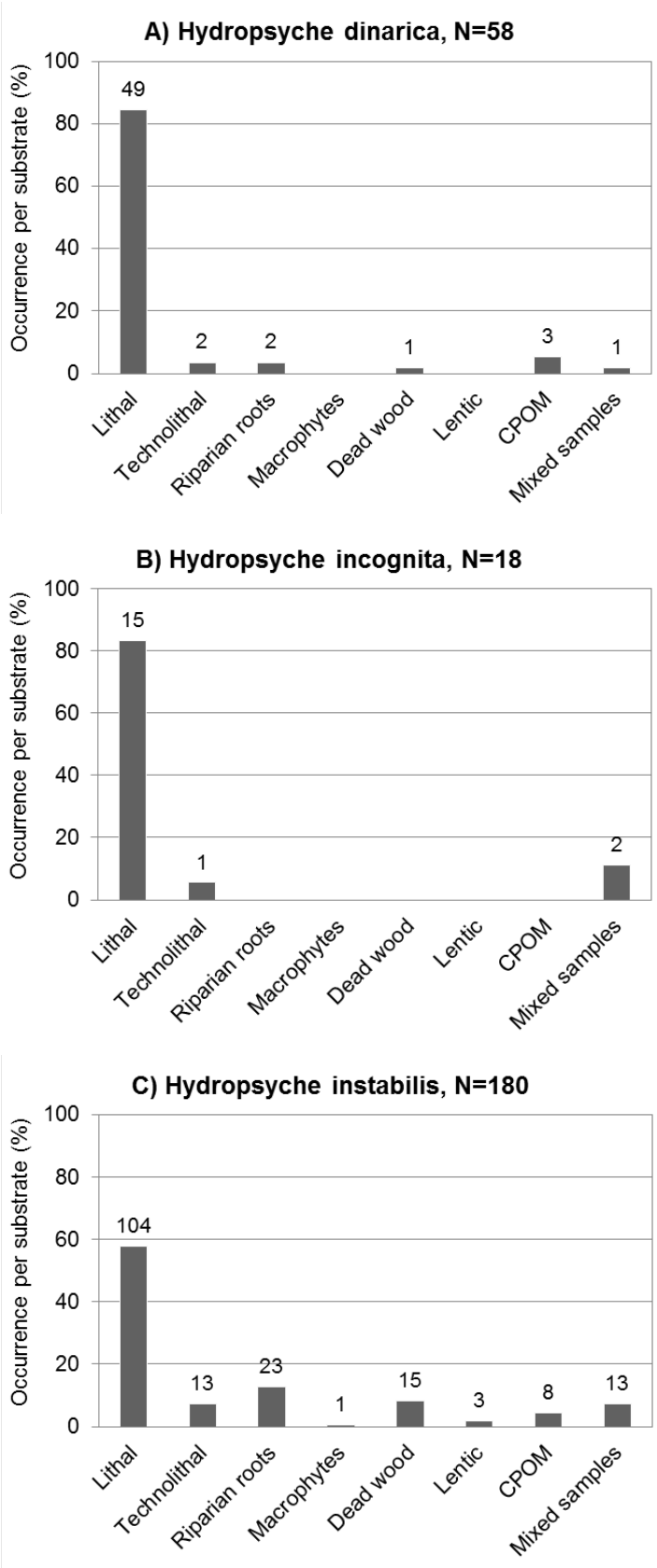

Figure 3.34: Substrate preference of the three *Hydropsyche* species (%) based on the field campaigns 2010 and 2011. The total number of occurrence sites is given as N. The number of occurrence sites per substrate is given as numbers above the bar, respectively.

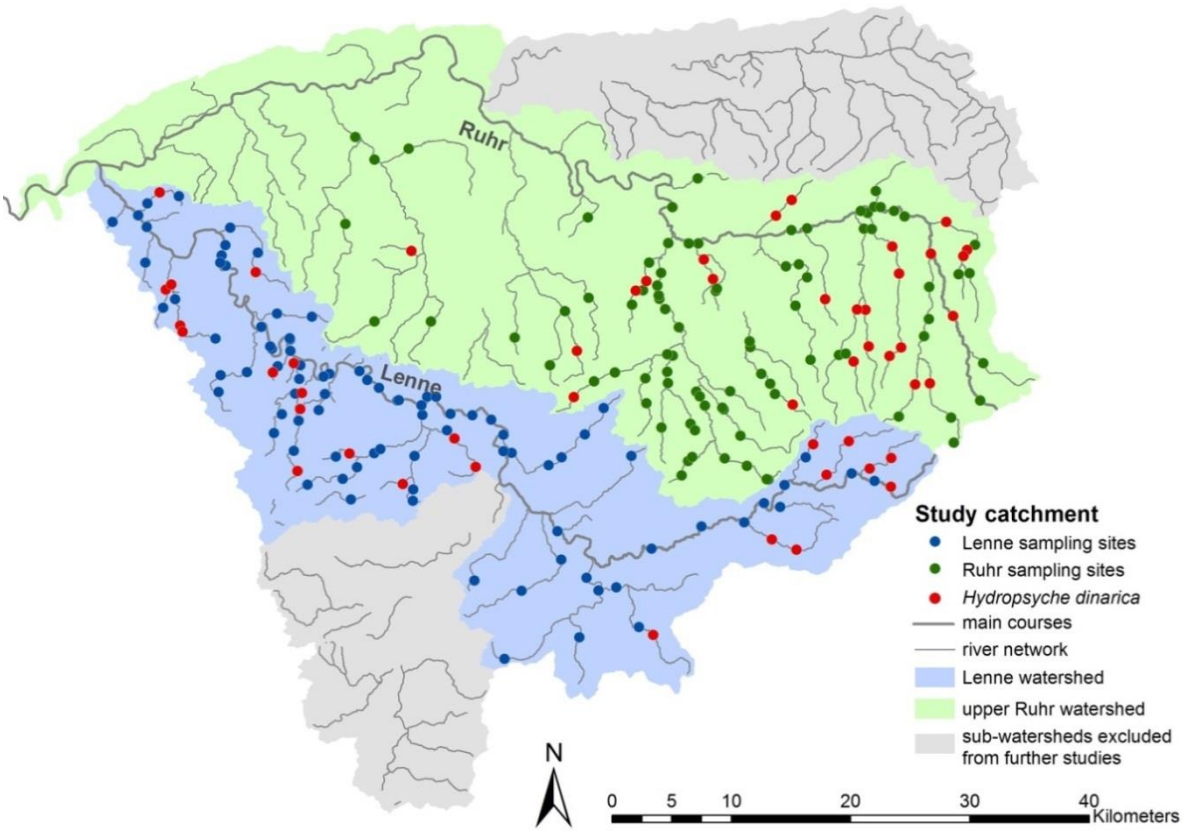

Figure 3.35: Occurrence sites of *H. dinarica* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *H. dinarica* was recorded present are given in red.

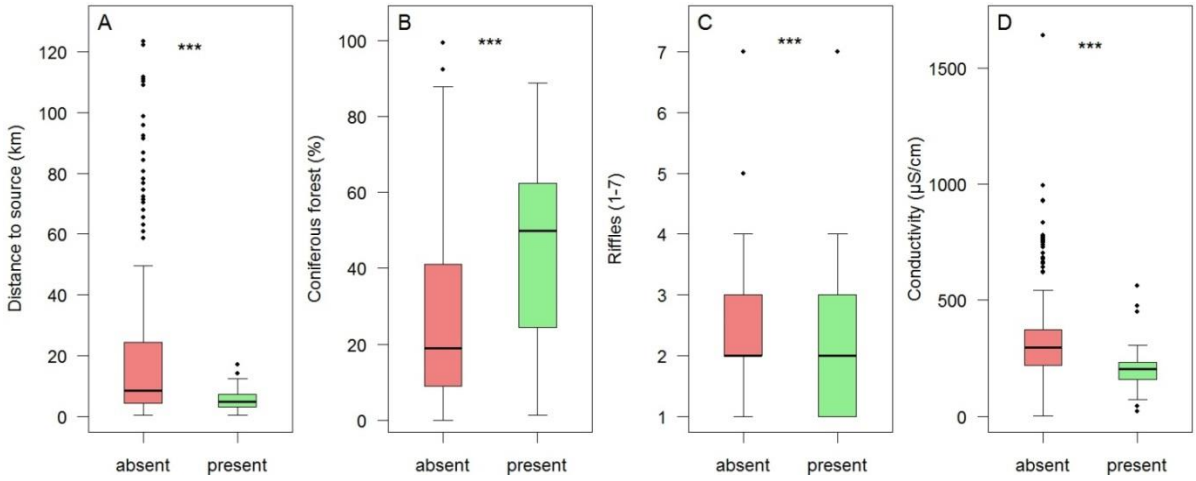

Figure 3.36: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *H. dinarica*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Physical habitat quality variables are given in categories ranging from classifications 1 (no alteration) to 7 (complete alteration). Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

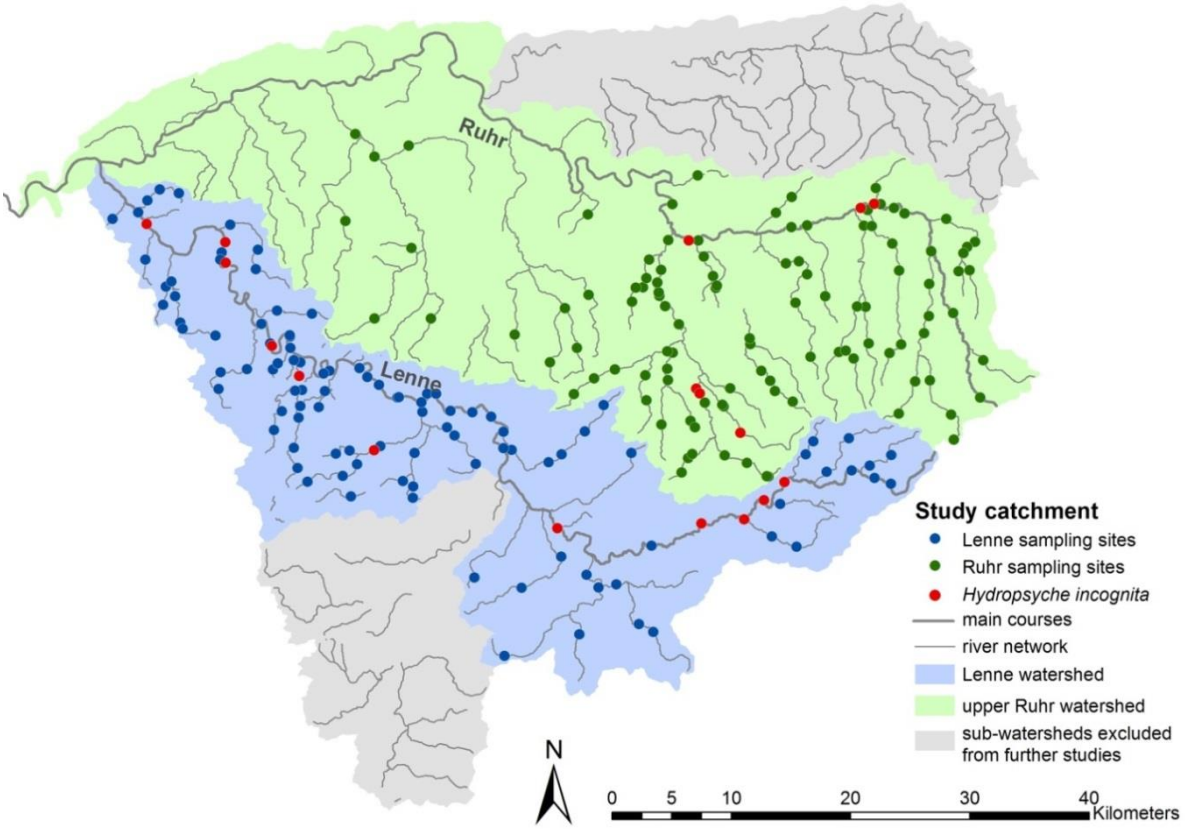

Figure 3.37: Occurrence sites of *H. incognita* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *H. incognita* was recorded present are given in red.

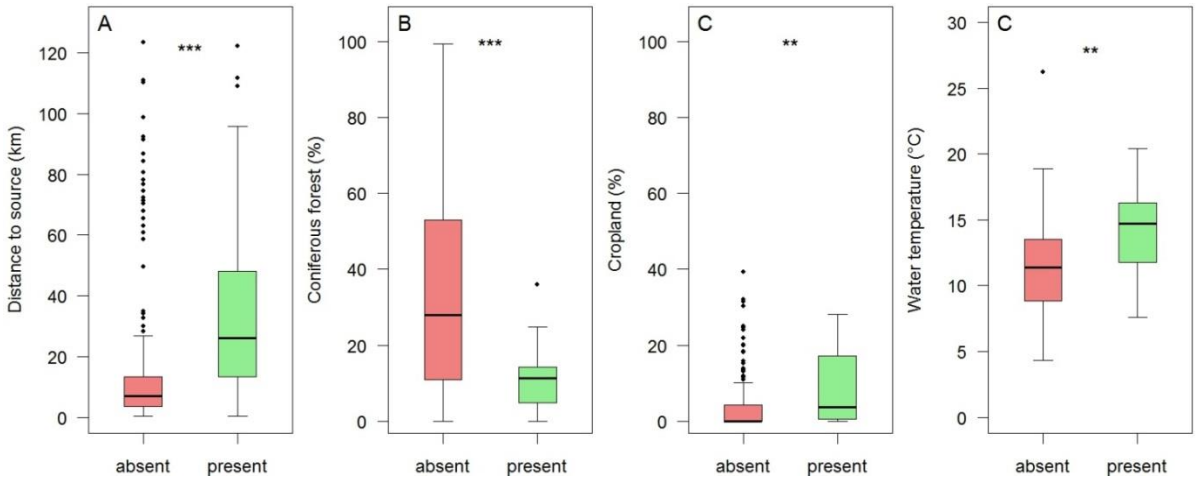

Figure 3.38: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *H. incognita*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

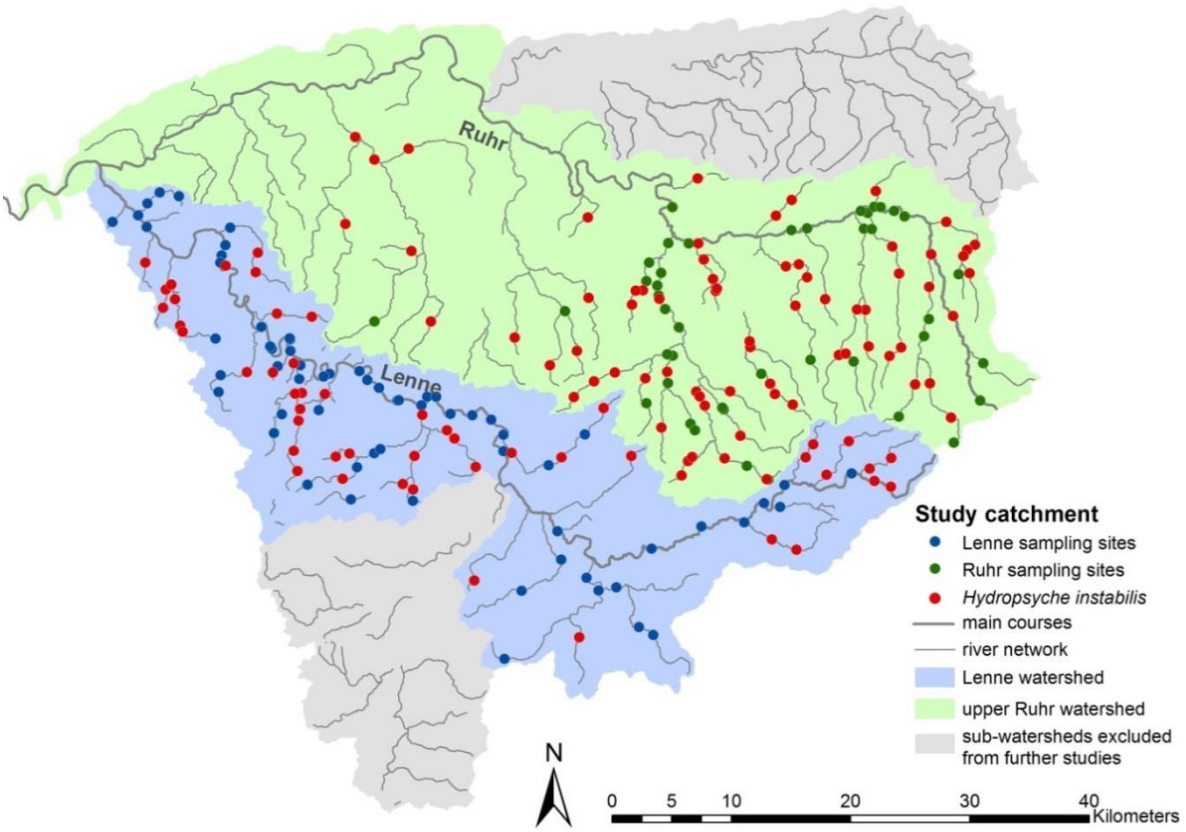

Figure 3.39: Occurrence sites of *H. instabilis* larvae in 2010 and 2011. All sampling sites are given as blue (Lenne) and green (Ruhr) dots. Sites at which *H. instabilis* was recorded present are given in red.

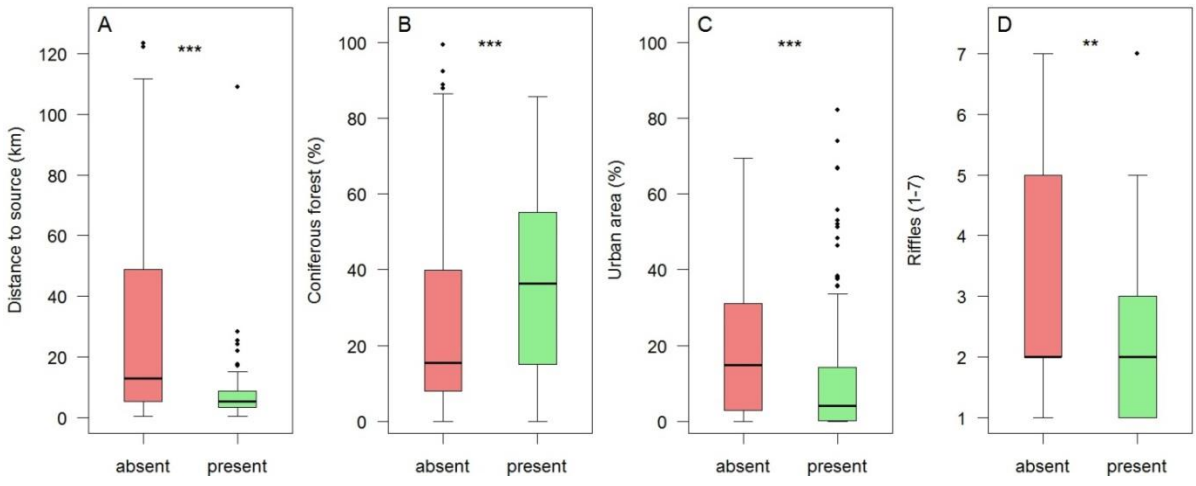

Figure 3.40: Boxplots of environmental variables that significantly distuingish between absence (red) and presence (green) of *H. instabilis*, based on the entire data set of in total 225 sampling sites. Medians are given as horizontal lines. Physical habitat quality variables are given in categories ranging from classifications 1 (no alteration) to 7 (complete alteration). Significance was tested using a Mann-Withney U-Test with significance levels p>0.05 n.s., p<0.05 *, p<0.01 ** and p<0.001 ***.

Further, all three *Hydrospyche* species prefer micro- and macrolithal, macrophytes and woody debris (Graf et al. 2008). The species were most frequent on lithal substrates (up to 80%) but *H. instabilis* did also occur on various organic substrates to a reliable extent (Figure 3.34).

Stream zonation preferences of the three hydropsychids strongly overlap showing strong preference to rhithral zones (Graf et al. 2002a). According to Valladolid et al. (2007) *H. instabilis* and *H. dinarica* are mainly distributed in rhithral stream sections (epi – metarhithral), whereas *H. incognita* also inhabits epipotamal sections (Graf et al. 2002a, Statzner & Dolédec 2011). Concordant to this, *H. dinarica* and *H. instabilis* showed a strong overlap in their distribution in streams with less than 20 km in distance to the source while *H. incognita* was also found in river stretches with up to 50 km in distance to source (Figure 3.36, Figure 3.38, Figure 3.40). However, *H. instabilis* does not occur in crenal stream zones (Edington & Hildrew 1981).

The presence of all hydropsychids was significant to the availability of coniferous forest within the riparian zone (Figure 3.36B, Figure 3.38B, Figure 3.40B) which may be a cross-relation to small, cold, oxygen-rich streams as coniferous forest dominates the upstream river stretches in the mountainous Ruhr catchment.

4 Modelling and transferring macroinvertebrate distribution models using broad-scale predictors

---

Parts of this chapter are published in the Special Issue '*Models of Freshwater Ecosystems: new approaches for ecological science and management*' of the Journal Fundamental and Applied Limnology.

Reference:

Gies, M., Sondermann, M., Hering, D. & Feld, C.K. Are species distribution models based on broad-scale environmental variables transferable across adjacent watersheds? A case study with eleven macroinvertebrate species. Fundamental and Applied Limnology 186/1-2, 63–97.

4.1 Introduction

For determining species distribution more precisely and to predict future distribution patterns, species distribution models (SDMs) are successfully applied in addition to monitoring activities. Especially for large-scale predictions in relation to changing environmental conditions (e.g., climate change, species invasions), SDMs provide useful information on possible range dynamics of species. The underlying data of large-scale SDMs are usually of a proximate nature, i.e. they are taken from broad-scale data sources such as nationwide surveys of land use or climate. These broad-scale environmental conditions affect aquatic ecosystems and thus be suited as proxies for fine-scale habitat conditions with more direct influences on species' occurrences.

Reliable models covering reasonable ranges of environmental variables and predicting species distributions at acceptable levels are also a prerequisite for model transferability. 'Transferability' (also called 'generalizability' or 'generality') concerns the ability of a model calibrated in one area to extrapolate useful predictions to another area (Miller et al. 2004, Phillips 2008). Successful transferability of species distribution models is potentially an efficient tool for biological conservation, saving time and personnel effort for sampling large areas and evaluating data. Models have been transferred to other regions for terrestrial species like plants (Randin et al. 2006, Ervin & Holly 2011), amphibians (Zanini et al. 2009), mammals (McAlpine et al. 2008, Barbosa et al. 2009, Murray et al. 2011, Tuanmu et al. 2011, Acevedo et al. 2014) and birds (Peterson et al. 2007, Zharikov et al. 2007), while respective approaches in aquatic ecosystems are mainly limited to fish distributions (Thomas & Bovee 1993, Freeman et al. 1997, Glozier et al. 1997, Sundblad et al. 2009, Wenger & Olden 2012). Freeman et al. (1997) demonstrated successfully transferable distribution models for freshwater fish between regulated and non-regulated streams, and suggested that transferability success was higher for fish with more specific habitat requirements. In contrast, Glozier et al. (1997) presented that the habitat preferences of a fish can be stream-specific and thus, that the transferability potential between river systems may be low. Sundblad et al. (2009) illustrated that transferability success can be influenced by area-specific differences in the range of the predictor variables and demonstrated the necessity of validating model predictions properly. To my knowledge, only a single study deals with the transferability of aquatic macroinvertebrate models. Here, Lamouroux et al. (2013) found that hydraulic models could predict taxa density variations in independent surveys for up to 60% of all cases but the degree of transferability was highly variable across taxa.

However, neither studies on the applicability of broad-scale environmental factors nor detailed research on the transferability of macroinvertebrate SDMs have yet been performed. As macroinvertebrate communities are widely used for monitoring river degradation and

restoration, e.g., for the European Water Framework Directive (Dir. 2000/60/EC, European Commission 2000), knowledge on model transferability between catchments would be beneficial for predicting the outcome of restoration and mitigation measures in a more standardized way. SDMs targeting macroinvertebrates can therefore provide more information about species-specific habitat requirements and detect potential source populations for assessing their recolonisation capacities of restored river sections.

In this study, SDMs for eleven aquatic macroinvertebrate species were developed in two adjacent river watersheds of similar characteristics. The first aim of this study was to test the suitability of broad-scale environmental variables derived by national surveys for developing reliable distribution models. Broad-scale variables that were available across both watersheds at the same data quality level (physical habitat structure, riparian land use) were used as environmental predictors. The models were compared between watersheds according to their model accuracy and their predictive performance. I secondly tested if model performance was improved by including locally measured physico-chemical measures and substrates. The third aim was to test generalizability of macroinvertebrate SDMs, i.e. whether a species distribution model developed in one area can be extrapolated to an adjoining area. The models best performing in individual watersheds were applied to the adjacent watershed. The implications of the results for using broad-scale instead of local predictors in distribution modelling approaches and transferring macroinvertebrate models in general are discussed.

4.2 Materials and methods

4.2.1 Data base

The study area was geographically separated into two major watersheds of similar expansion: the upper Ruhr and its main tributary Lenne (Figure 4.1). The full data set of in total 225 sampling sites (2010: 60 Lenne and 61 upper Ruhr; 2011: 52 Lenne and 52 upper Ruhr) originating from two field campaigns in spring (April – mid June) 2010 and 2011 was therefore split up spatially. For each watershed, SDMs were generated using two groups of broad-scale environmental variables for the SDMs: variables describing physical habitats and percentages riparian land use in two buffer widths (10 m and 100 m on each bank side). Hydromorphological variables were derived from the national hydromorphological survey for those 100 m sections, in which sites were located (see chapter 2.4). The number of assessment scores (Appendix 1d) was reduced due to lacking gradients or lacking data (Appendix 2a and 2b). The physical habitat quality variables used for modelling are indicated in Table 4.1. Here, 21 out of the total 25 single attributes were used as potential predictors of species distribution.

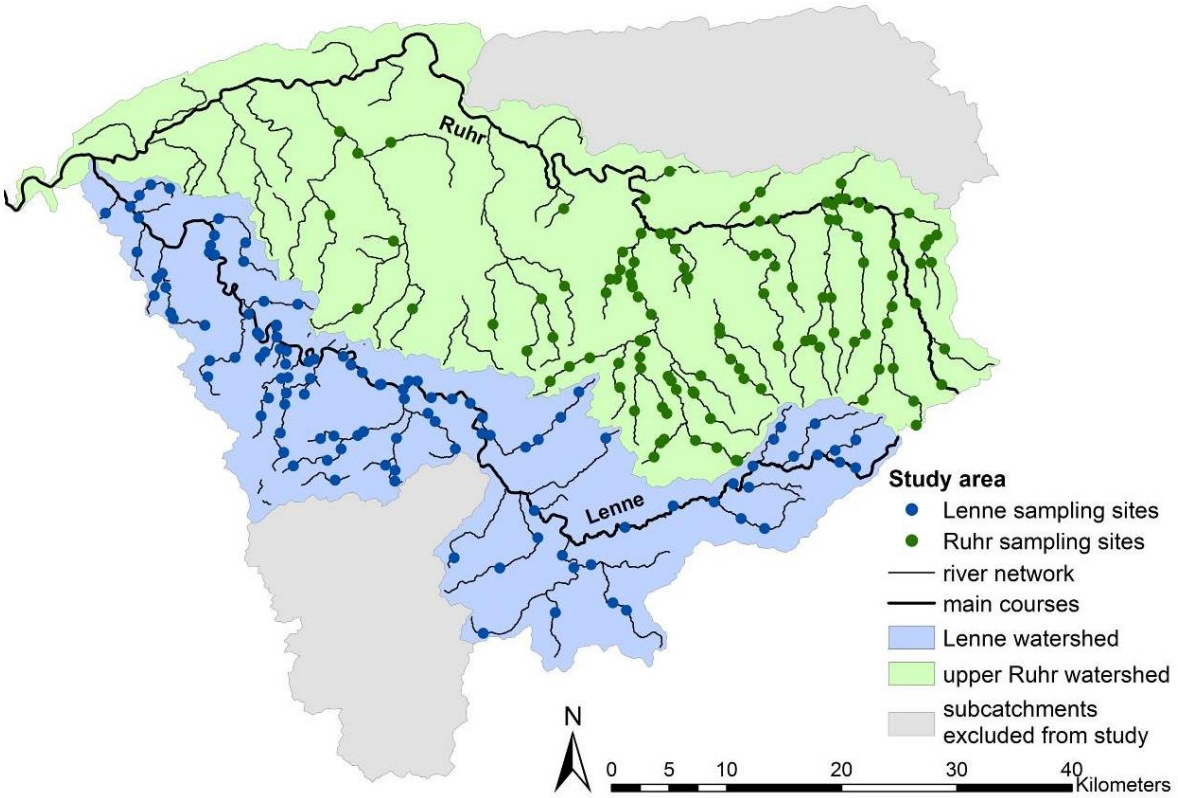

Figure 4.1: Study area and sampling sites in the model catchment of River Ruhr, Germany. The white sub-watersheds represent the Bigge (Lenne) and Moehne (Ruhr) watershed that were excluded from this study because of hydromorphological and water quality impacts caused by reservoir lakes in the continuum.

Table 4.1: Environmental variables on hydromorphology, riparian land use and local (fine-scale) variables which were included into the distribution models. Hydromorphological variables are based on the German physical habitat quality survey that includes structural in-stream variables as well as variables on the riparian condition. Riparian land use variables are based on the German Official Topographical Cartographic Information System (ATKIS).

		Environmental parameters		Abbreviation
Physical habitat quality	Channel bed features	Mean water depth		MWD
		Planform		PlanForm
		Erosion at bends		Erosion
		Bars		Bars
		Features indicating natural channel dynamics (e.g. wood jams, island, widening)		FeatDyn
		Riffles and steps		Riffles
		Flow diversity		FlowDiv
		Depth variability		DepVar
		Substrate diversity		SubsDiv
		Channel features (e.g. scour- and backwater pools, rapids, cascades)		FeatChan
	Channel bank features	Cross-section form		CrSecForm
		Cross-section depth		CrSecDep
		Bank erosion (indicating widening of channel)		BankEro
		Cross-section width variability		CrSecWid
		Riparian vegetation		RipVeg
		Bank protection		BankProt
		Bank features (e.g. woody debris, undercut banks)		FeatBank
	Floodplain	Land-use		Landuse
		Riparian buffer strip		RipBuff
		Infrastructure works (e.g. roads, dumping sites, fish-farms)		Infrastruc
		Local situation (urban/landscape)		LocSit
Land use categories by ATKIS		Cropland (%)	10 m on each bank side (narrow)	Crop_n
			100 m on each bank side (wide)	Crop_w
		Extensive/pasture (%)	10 m on each bank side (narrow)	Ext_n
			100 m on each bank side (wide)	Ext_w
		Deciduous forest (%)	10 m on each bank side (narrow)	DecFor_n
			100 m on each bank side (wide)	DecFor_w
		Coniferous/mixed forest (%)	10 m on each bank side (narrow)	ConFor_n
			100 m on each bank side (wide)	ConFor_w
		Urban/industrial area (%)	10 m on each bank side (narrow)	Urb_n
			100 m on each bank side (wide)	Urb_w
		Ratio %forest in 200 m buffer / %urban in 20 m buffer		F020U200
Fine-scale variables	Physico-chemistry	Water temperature (°C)		T_water
		Conductivity (µScm^{-1})		Cond
		Oxygen content (mgl^{-1})		O2_cont
		pH		pH
		Nitrate content (mgl^{-1})		NO3
		Chloride content (mgl^{-1})		Chlorid
	Substrates (% coverage)	Makrolithal (>20 - 40cm)		Macro
		Mesolithal (>6 - 20cm)		Meso
		Microlithal (>2 - 6cm)		Micro
		Akal (>0,2 - 2cm)		Akal
		Psammal/Psammopelal (>6µm - 2mm)		PsammPel
		Argyllal (<6µm)		Argyll
		Technolithal		Tech1
		Algae		Algae
		Macrophytes (submers and emers)		MP
		Living parts of terrestrial plants		LTTP
		Xylal (dead wood)		Xylal
		CPOM (coarse particulate organic material)		CPOM
		FPOM (fine particulate organic material)		FPOM

Climate variables were not considered as predictors because the spatial extent of this study was limited to a mountainous region without strong climatic differences. However, the distance to source was used as a proxy for water temperature accounting for indirect differences in stream temperature along the river courses.

In order to test the explanatory power of fine-scale environmental predictors, separate models were also conducted using local variables (physico-chemistry and coverage of river bottom substrates) in addition to hydromorphological alteration and land use (Table 4.1). This resulted in 32 environmental variables used for broad-scale SDMs and 51 environmental variables in mixed broad- and fine-scale SDMs (Table 4.1).

The SDMs aimed at predicting the distribution within the species' realized niche, i.e. the species' occurrence ranges within the environmental dimension that affects biotic interactions and thus, a species' fitness (Hutchinson 1957, see also Kearney (2006) for a detailed definition of niches in SDM approaches). Additionally, due to the geographical location of the Ruhr watershed, a strong difference in altitude and distances to source within the original data set was existent (Figure 4.2). I therefore selected species-specific subsets, including only those sites that fit the species' occurrence range along the river continuum (Schmidt-Kloiber & Hering 2012). This procedure avoids the modelling of species occurrences at river sections that fall out of the species' range of occurrence. To define the species' occurrence range along the river continuum, the distance to stream source was used as a proxy of stream size and determined the range of distances of all occurrences of each species ± 10% as a species natural occurrence range. Observed presence sites were not omitted. The species' ranges obtained by this procedure were cross-checked with the species' longitudinal zonation indicated by Schmidt-Kloiber & Hering (2012) (Table 3.2) and corresponded to the known species' occurrence range along the river continuum. Thus, all presences of a species were used to build the models but the prediction of species distribution was restricted to the area that falls into the species' range of occurrence (Table 4.2).

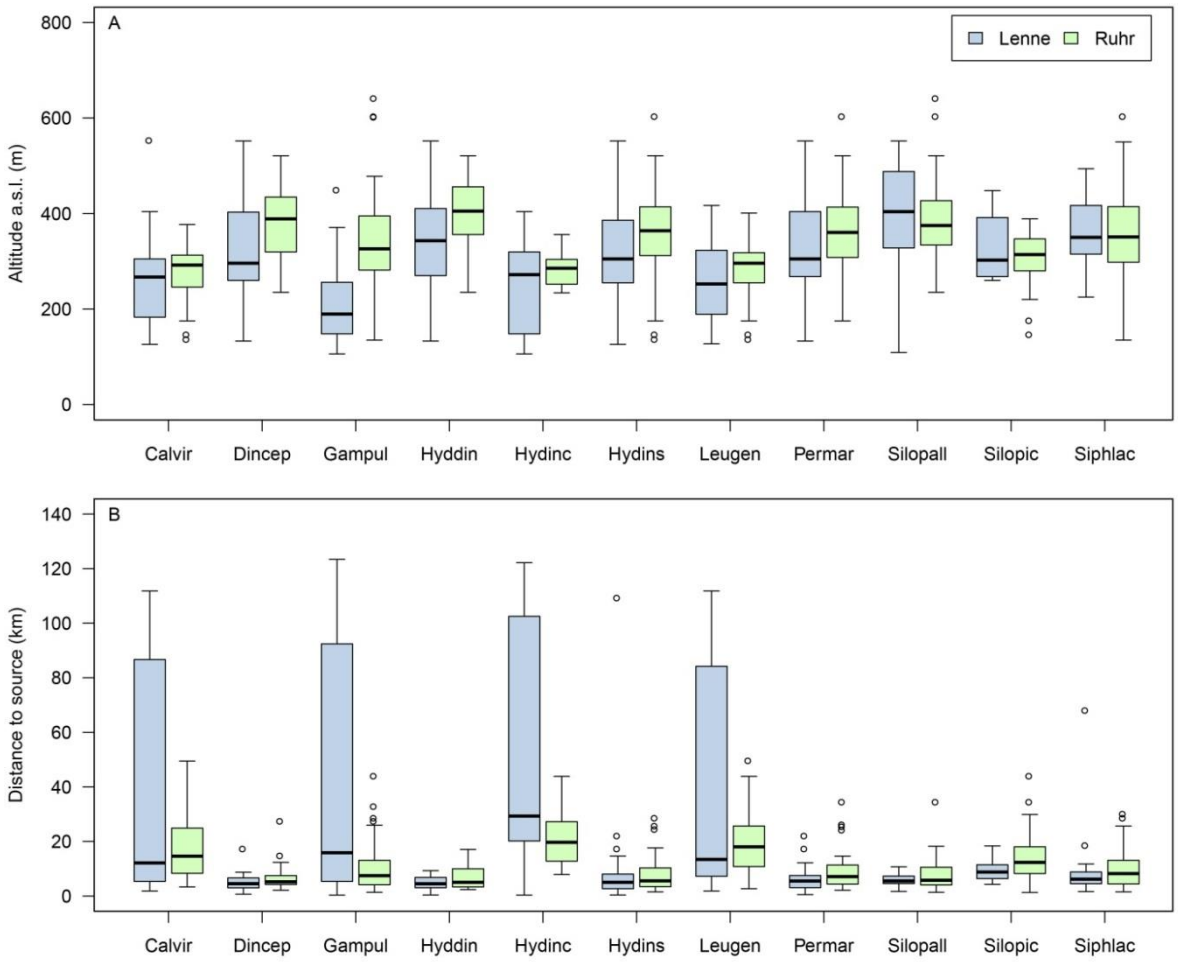

Figure 4.2: Range of altitude (A) and distance to source (B) per species and watershed based on the original raw data.

Table 4.2: Subsampling of original data in relation to the species' range in distance to source.

Model species	Min (-10%) in km	Max (+10%) in km	Range of distance to source (km)	Total number of subsamples	No. of Lenne subsamples	No. of Ruhr subsamples
Gampul	0.343 (0.034)	123.420 (12.342)	0.31 - 135.76	224	112	112
Siphlac	1.520 (0.152)	67.843 (6.784)	1.37 - 74.63	194	84	110
Calvir	1.856- (0.186)	111.805 (11.181)	1.67 - 122.99	207	99	108
Permar	0.528 (0.053)	34.223 (3.422)	0.48 - 37.65	190	80	110
Dincep	0.684 (0.068)	27.243 (2.724)	0.62 - 29.97	185	77	108
Leugen	1.856 (0.186)	111.805 (11.181)	1.67 - 122.99	207	99	108
Silopall	1.368 (0.137)	34.223 (3.422)	1.23 - 37.65	184	75	109
Silopic	1.313 (0.131)	43.846 (4.385)	1.18 - 48.23	185	75	110
Hyddin	0.369 (0.037)	17.064 (1.706)	0.33 - 18.77	172	78	94
Hydinc	0.343 (0.034)	122.199 (12.220)	0.31 - 134.42	224	112	112
Hydins	0.369 (0.037)	109.088 (10.909)	0.33 - 120.00	222	110	112

4.2.2 Species distribution modelling

Non-parametric multiplicative regression (NPMR) was used to determine the habitat requirements and to model the presence and absence of eleven species throughout the entire model catchment (section length: 100 m). Please see chapter 2.5.1 for a detailed description of the NPMR method.

Separate models were set up for both watersheds (Lenne and upper Ruhr) using local mean models and a Gaussian weighting function. The distance-weighted Gaussian probability function is applied to obtain a response estimate for a given predictor. The minimum average neighborhood size N*, i.e. is the average sum of the weights for other data points that bear on the target point, was automatically set to 0.05 (5% of the total sampling units) during the modelling procedure and to N* = 1 (100% of the sampling units) during the prediction procedure.

Model fit in NPMR is described as log likelihood ratio (logB), with the highest value indicating the best model. The goodness of fit of a nonparametric regression model is described by pseudo-R^2 (xR^2), a cross-validated coefficient of determination, which is equivalent to the linear R^2 describing the ratio of explained variance of the model. The cross-validated AUC gives information about a model's predictive power, i.e., how well the model discriminates presences and absences by comparing predicted results to observations (Hanley & McNeil 1982, Vaughan & Ormerod 2005). According to Araújo et al. (2005) AUC values ≥ 0.80 indicate a 'good discrimination quality' (see also Swets 1988). The relative influence of a predictor variable within a model (sensitivity) was identified iteratively, estimating the model's changes when adjusting individual predictor's observed values up and down in 5% steps (McCune 2006, McCune 2007).

4.2.3 Model transferability across watersheds

The NPMR technique allows a prediction of a species' probability of occurrence at new sites implementing the given environmental variables. The prediction of probability of species' occurrences was applied on the regional river network which is provided by the physical habitat survey. The study catchment covers in total 10,701 river sections in 100 m in length (watersheds of Bigge and Moehne excluded). Small and medium sized rivers (type 5) comprehend 10,342 sections (4,328 Lenne sections, 6,014 upper Ruhr sections). Streams comprehend 359 sections (main course of the Ruhr). For each 100 m section, probabilities of occurrence ranging between 0 and 1 were produced for every model species considering the predictor variables selected by the SDM. These estimates can be interpreted as the percentage of habitat suitability within this river section. For NPMR prediction, a conservative scenario and an average neighborhood size of 1 was used.

The best SDMs were used for prediction of probabilities of occurrence within and between watersheds. Within-watershed prediction comprises an internal evaluation approach applying Lenne SDMs to all sites of the Lenne watershed and Ruhr SDMs to all sites of the Ruhr watershed. The between-watershed prediction comprises therefore an external evaluation applying Lenne SDMs to all sites of the Ruhr watershed and vice versa.

Predictive maps (habitat suitability maps) were then generated in ArcGIS 10 (ESRI 2011) taking into account the species specific subsampled range in distance to source. To better visualize realistic probability of occurrence was classified in 3 classes: low habitat suitability with values ranging between 0.00 – 0.39 (red), intermediate suitability with a range of 0.40 – 0.59 (grey) and high suitability with probabilities ≥ 0.60 (green). River sections for which a prediction has not been possible due to missing data predictions was set to NA.

The transferability of model results between both watersheds was evaluated using the transferability index (TI) developed by Randin et al. (2006):

$$TI = \frac{\frac{1}{2}\left[\left(1 - \frac{\left|AUC_{regionA \rightarrow regionA} - AUC_{regionA \rightarrow regionB}\right|}{0.5}\right) + \left(1 - \frac{\left|AUC_{regionB \rightarrow regionB} - AUC_{regionB \rightarrow regionA}\right|}{0.5}\right)\right]}{1 + \left|\left|\frac{AUC_{regionA \rightarrow regionA} - AUC_{regionA \rightarrow regionB}}{0.5}\right| - \left|\frac{AUC_{regionB \rightarrow regionB} - AUC_{regionB \rightarrow regionA}}{0.5}\right|\right|}$$

with $AUC_{regA \rightarrow regA}$ and $AUC_{regB \rightarrow regB}$ indicating a model fitted and evaluated in region A and B, respectively, and $AUC_{regA \rightarrow regB}$ and $AUC_{regB \rightarrow regA}$ indicating a model fitted in one region and applied to another region. The TI thereby indicates the decrease of AUC coefficients when switching from within-watershed ($AUC_{regA \rightarrow regA}$ and $AUC_{regB \rightarrow regB}$) to between-watershed ($AUC_{regA \rightarrow regB}$ and $AUC_{regB \rightarrow regA}$) evaluation. The index ranges 0–1, with 1 indicating full transferability of models between the two watersheds. In this study, I evaluated the model's internal fit using the leave-one-out cross-validation procedure on a watershed-specific model training data and then evaluated the external fit by projecting the model results (presence/absence) on the other watershed, thus comparing the projected predictions with independent observations (Figure 4.3).

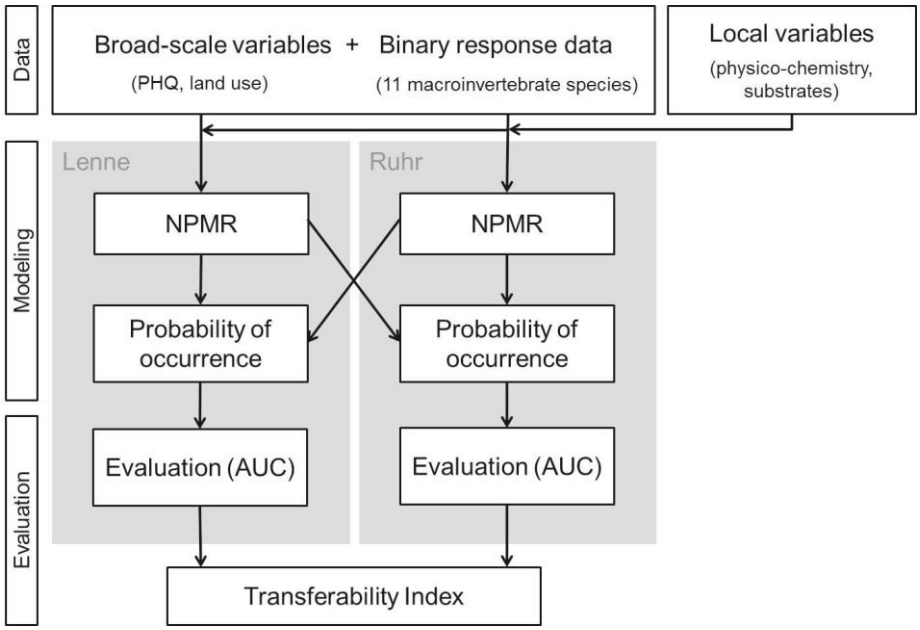

Figure 4.3: Conceptual analytical approach of this study.

4.2.4 Statistical analysis

All subordinate statistics and graphics were run in R 2.14.2 (R Development Core Team 2012). Spearman correlation coefficients and variance inflation factors were calculated to check for multi-collinearity between explanatory variables (package 'usdm' by Naimi 2013). Differences in environmental variables between watersheds were analysed using a mixed principal components analysis (mPCA; Hill & Smith 1976) using the library 'ade4' (Dray & Dufour 2007) and a Student's t-test for testing significance. Significance of watershed differences in model input variables was tested using a Mann-Whitney U-test (with Bonferroni correction, significance level $p<0.05$, * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$).

4.3 Results

4.3.1 Environmental variables in both watersheds

Though land use patterns are relatively similar in the Lenne and Ruhr watersheds, the floodplains of the Lenne and its tributaries are not only urbanized but also industrialized. Although legacy contamination (heavy metals) may be present in some patches of the upper Ruhr catchment, the water quality of the entire watershed is good (Ruhrverband 2009; 2013) but diffuse pollution (nitrogen, phosphorous) from agriculture is still present, predominantly in the lower potamal sections of the river network (up to 42% agriculture, up to 38% urban areas in sub-watersheds). Land use is largely dominated by forestry (coniferous forest with up to 70% in upper rithral parts of the catchments), with agriculture and urbanization occurring mainly along larger valleys. Land use within the riparian zone (200 m in width on each bank

side) is dominated by coniferous forest (up to 44%), pasture (up to 24%) and deciduous forest (10-13%). Due to the regional history in steel and wire industry, the Lenne watershed is governed by a higher percentage up to 15% of urban (especially industrial) areas (Figure 4.4A).

Despite the overall good water quality, other sources of degradation are prominent in the entire Ruhr system, namely physical habitat degradation due to various and long-term human impact, namely water abstraction, impoundments, bank and bed fixation and riparian modification (LUA & MUNLV 2005, MUNLV 2005). This leads to a high proportion (up to 70%) of clearly to excessively affected river sections at a scale of 100 m whereas only 9-14% of all river sections remain near-natural to conditionally near-natural (Figure 4.4B).

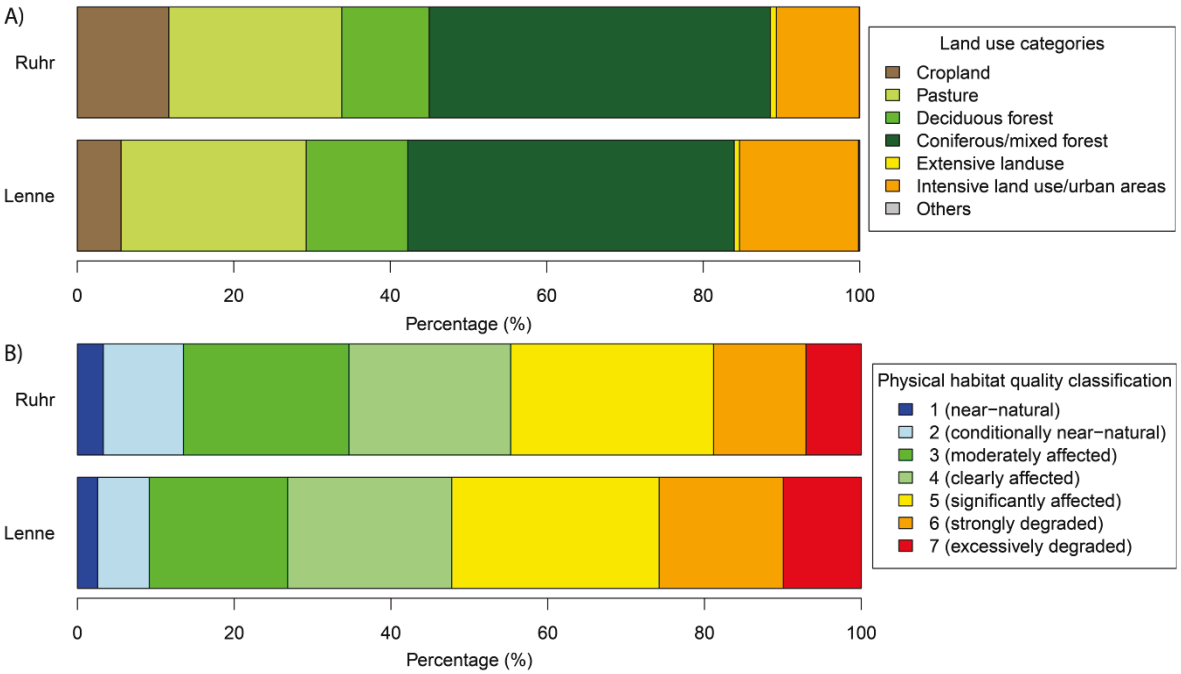

Figure 4.4: (A) Percentages of land use categories within a 200m riparian buffer strip along the river network within the study area. Water bodies were excluded from this analysis. (B) Percentages of physical habitat quality assessment derived by the national hydromorphological survey in 2009 of the North Rhine-Westphalia State Agency for Nature, Environment and Consumer Protection (LANUV).

The main River Lenne is characterized by a high number of technical transverse structures (60 weirs in total), mostly associated to hydro-electric power stations, and consequently, impoundment reaches and residual water sections determine the discharge regime of the watershed (Figure 4.5). Within the entire study area, most of the tributaries are additionally affected by smaller weirs influencing the runoff. Degradation level increases in the riparian zones and water banks along the water course due to arising proportion of urban and industrial areas. Thus, the Lenne watershed is influenced by hydromorphological degradation and fragmentation which determine the distribution of sensitive macroinvertebrates. Impoundment

and residual water sections in the main river course play a minor role in the Upper Ruhr watershed contrast to the Lenne watershed.

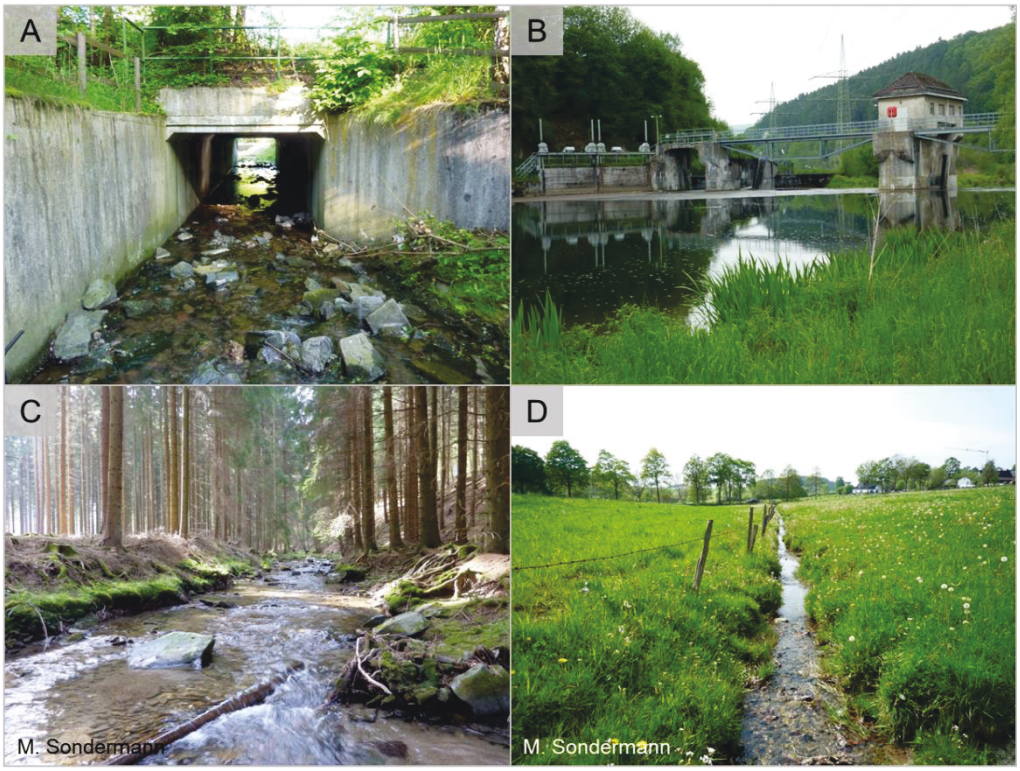

Figure 4.5: Examples of river alterations in the Lenne and Ruhr watershed: A Rahmede at Lüdinghausen (river type 5, high level of degradation), B water power plant at Eilringhausen retaining the Lenne main course on a length of 2.5-3.0km, C Elpe at Gevelinghausen flowing through afforested coniferous forest, D extensive land use directly adjoining to the river course (Wenne at Obringhausen, river type 5).

A Spearman correlation (Appendix 2c) and VIF analysis (Table 4.3) of all used variables showed neither correlation nor multi-collinearity between all 51 variables or between broad-scale and local variables. Land use classes regarding two buffer sizes showed inter-correlation (R >0.70) of narrow and wide buffer strips. Additionally, land use classes in wide riparian buffers showed collinearity due to the fact that wide buffer sizes contain the narrow ones (Table 4.3). However, I did not exclude these variables from further analyses as these land use buffer strips obtain valuable information on riparian surroundings and related indirect factors on stream conditions (e.g. diffuse pollution). The ratio of urban and forest land use (Fu020U200) correlated to percentages of coniferous forest and urban areas as this ratio is calculated based on these LN classes (Table 2.4). However, the VIF value was low.

Table 4.3: VIF values for the explanatory variables (fine-scale, land use and hydromorphological variables). Large VIF values compared to the others indicate high collinearity of those predictors (Zuur et al. 2007). Land use classes in 200 m buffer strips showed high multicolinearity due to their intercorrelation with narrow buffer strips (**bold**).

Local variables	VIF	Land use variables	VIF	Physical habitat quality variables	VIF
Makro	18.035	DecFor_n	2.921	LocSit	2.521
Meso	26.122	ConFor_n	10.753	MWD	3.779
Mikro	23.591	Ext_n	7.995	Planform	2.856
Akal	8.886	Crop_n	3.273	Erosion	3.278
PsammPel	1.900	Urb_n	6.193	Bars	2.571
Argyll	4.217	**DecFor_w**	**232.892**	FeatDyn	2.142
Tech1	11.221	**ConFor_w**	**1112.939**	Riffles	3.069
Algen	1.526	**Ext_w**	**758.126**	FlowDiv	3.313
MP	1.374	**Crop_w**	**81.324**	DepVar	2.076
LTTP	1.813	**Urb_w**	**659.922**	SubsDiv	2.367
Xylal	1.878	F020U200	3.512	FeatChan	3.050
CPOM	1.551			CrSecForm	3.722
FPOM	1.477			CrSecDep	3.837
T_water	2.428			BankEro	3.769
LF	1.924			CrSecWid	2.706
O2_cont	1.696			RipVeg	1.893
pH	2.041			BankProt	2.398
NO3	1.711			FeatBank	1.966
Chlorid	1.809			Landuse	1.751
				RipBuff	1.765
				Infrastruc	1.648

Thirteen hydromorphological variables and six land use variables were subjected to a mixed PCA in order to identify watershed-specific differences in the dataset. The first mixed PCA axis (mPCA 1, explained variance: 26%) was mainly describing a hydromorphological gradient (Figure 4.6A), while mPCA 2 (explained variance: 12%) described a land use gradient. Although the location of sites from both watersheds in the PCA plot significantly differed (Figure 4.6B, t-Test: $p < 0.001$), the strong overlap of sites of both watersheds in the ordination biplot suggests that physical habitat and land use impacts in both watersheds were similar to a certain degree (see Appendix 2a and 2b).

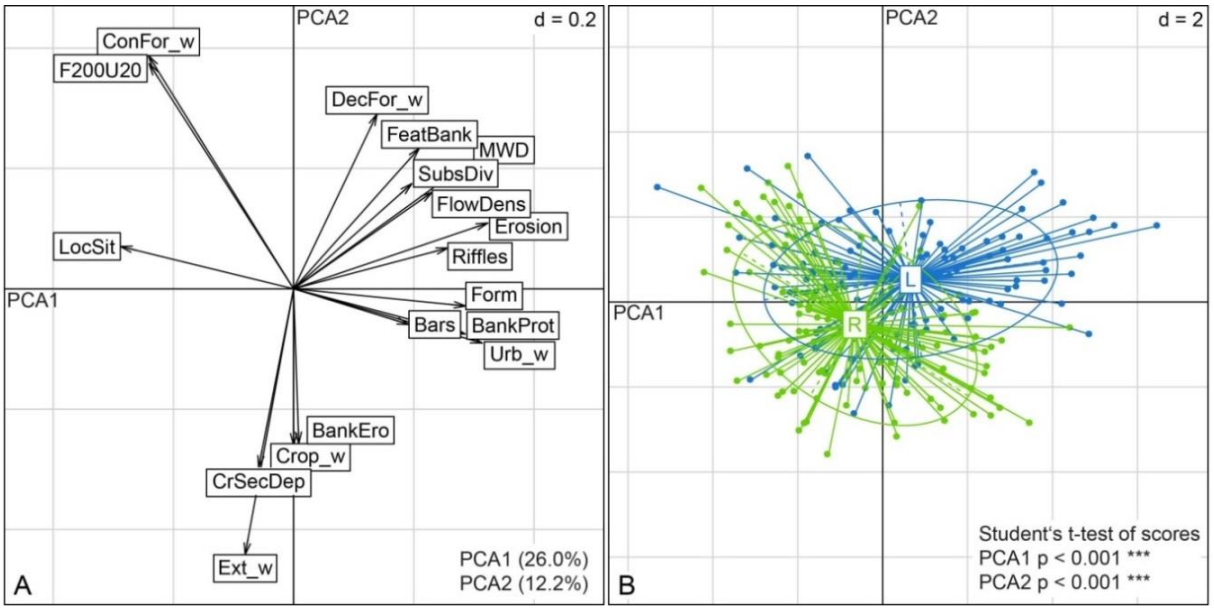

Figure 4.6: Mixed PCA of environmental variables. A: biplot of variable loadings, B: biplot of scores categorized by watersheds (blue = Lenne watershed (L), green = Ruhr watershed (R)). For abbreviations of the labels, see Table 2.3 and Table 2.4.

4.3.2 Species distribution models

According to the species-specific subsets limited to those parts of the longitudinal continuum reflecting the species' natural ranges, the species' prevalences throughout both watersheds were calculated. Species' occurrences were moderate ranging from 6% (*H. incognita* in the Ruhr watershed) to 63% (*H. instabilis* in the Ruhr watershed, Figure 4.7).

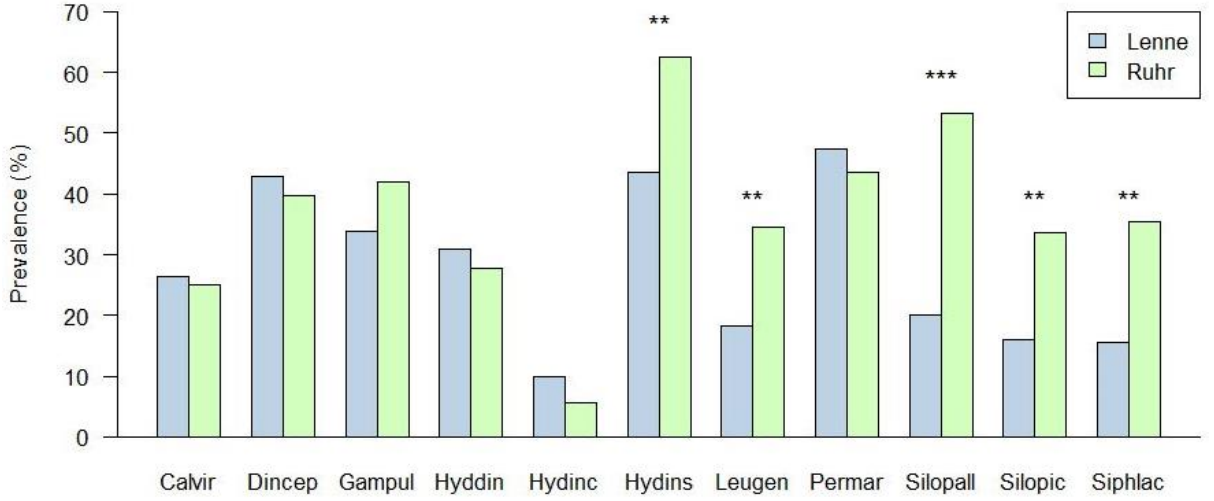

Figure 4.7: Prevalence of model species after subsampling. Significance between both catchments was tested by Chi2-test using significance levels * = p<0.05, ** = p<0.01, *** = p<0.001.

From the 25 hydromorphological variables, 21 were chosen as potential predictors offering a useful gradient within both watersheds (Table 4.1). LogB values ranged 1.92–9.75 for the Lenne models and 3.65–7.56 for the Ruhr models, respectively (Table 4.4 and Table 4.5). The pseudo R^2 values (xR^2) achieved up to 0.379 in the Lenne watershed and 0.305 in the Ruhr watershed. Opposed to these measures, the AUC was reasonably good (0.78–0.84) for several species (*D. cephalotes, H. instabilis, L. geniculata, S. piceus, S. lacustris*), thus indicating interpretable results of the cross-validation procedure inherent to NPMR. Although *H. incognita* models showed low model performances (xR^2: 0.212 and 0.173), the AUC value was the highest in both watersheds (0.89 and 0.90).

No consistent preference of one variable group over another was found when evaluating the environmental variables in the models. The model of *H. instabilis* for the river Lenne, for example, included five physical habitat variables, but no land use variables, while the SDM for *D. cephalotes* revealed its strong relation to riparian coniferous forest. In contrast, *L. geniculata* showed the highest logB value in the Ruhr watershed, with percent urban area as the main predictor.

When plotting species-specific logB and AUC values of the Lenne against the Ruhr watershed, several species were found to perform either well in both watersheds (e.g., *D. cephalotes*), while others performed better in the Lenne (e.g., *H. instabilis*) or in the Ruhr watershed (e.g., *L. geniculata, S. piceus, S. lacustris*) (Figure 4.8, black points). Yet, the differences in AUC were not significant (t-test: $p = 0.06$; $t20 = 0.84$).

The inclusion of 19 local environmental variables (physico-chemistry, substrates) into the distribution models improved model accuracy and predictive performance of some species which performed weak before, especially *C. virgo* and *P. marginata* in the Lenne watershed, *H. dinarica* and *S. pallipes* in the Ruhr watershed and *D. cephalotes* in both watersheds (Figure 4.8, white points). In these models, broad-scale predictors were partly replaced by local predictors (Appendix 2f). In some cases, however, model performances decreased when local predictors were included (*L. geniculata* in the Lenne watershed, *G. pulex*, *P. marginata* and *H. instabilis* in the Ruhr watershed). Models of *H. incognita* showed no difference following inclusion of local predictors. Mean absolute improvement of logB throughout all species in the Lenne watershed was +0.79 ± 1.05, in the Ruhr watershed +0.52 ± 1.25. Mean improvement of AUC values was +0.03 (± 0.10 in the Ruhr watershed, ± 0.04 in the Lenne watershed) in both watersheds.

Table 4.4: Model results of the Lenne watershed including logB values, all detected predictors and their tolerance and sensitivity. **bold**: two highest logB and xR^2 values.

Response variable	No. of samples	logB	xR^2	Predictors	Tolerance	Sensitivity	AUC
Gammarus pulex	112	4.61	0.207	RipVeg	1.50	0.28	0.75
				Riffles	2.10	0.19	
				Ext_n	34.00	0.17	
				Crop_w	9.81	0.07	
Siphlonurus lacustris	84	1.92	0.043	DecFor_w	4.11	0.43	0.71
				Landuse	0.60	0.39	
Calopteryx virgo	99	2.13	0.084	ConFor_w	4.28	1.54	0.69
				Urb_n	13.71	0.27	
				BankProt	4.20	0.10	
Leuctra geniculata	99	3.00	0.008	Urb_w	6.94	0.64	0.67
				FlowDiv	1.00	0.11	
Dinocras cephalotes	77	**5.32**	**0.266**	ConFor_w	9.93	0.72	0.78
				Bars	1.20	0.32	
				FeatChan	1.25	0.28	
				DecFor_n	27.72	0.09	
Perla marginata	80	3.66	0.030	ConFor_w	24.82	0.42	0.60
				RipVeg	0.30	0.13	
				ConFor_n	65.00	0.05	
				FlowDiv	2.80	0.03	
Silo pallipes	75	2.61	0.113	Ext_n	9.72	0.60	0.76
				FlowDiv	0.60	0.42	
Silo piceus	75	2.35	0.110	Ext_n	4.86	1.08	0.79
				Ext_w	11.50	0.20	
Hydropsyche dinarica	78	4.28	0.246	Ext_w	7.72	0.75	0.76
				ConFor_w	19.85	0.35	
				FeatBank	0.75	0.24	
Hydropsyche incognita	112	4.94	0.212	ConFor_w	4.96	1.15	0.89
				Riffles	0.60	0.54	
Hydropsyche instabilis	110	**9.75**	**0.379**	MWD	0.50	0.83	0.83
				CrSecDep	1.20	0.35	
				FeatBank	0.75	0.25	
				Planform	2.10	0.15	
				SubsDiv	1.95	0.03	

Table 4.5: Model results of the Ruhr watershed including logB values, all detected predictors and their tolerance and sensitivity. **bold**: two highest logB and xR^2 values.

Response variable	No. of samples	logB	xR^2	Predictors	Tolerance	Sensitivity	AUC
Gammarus pulex	112	5.98	0.203	Planform	0.60	0.67	0.72
				FeatBank	0.50	0.44	
				DecFor_n	23.83	0.10	
				ConFor_n	61.07	0.04	
				DepVar	3.75	0.02	
Siphlonurus lacustris	110	6.98	**0.286**	Ext_w	13.07	0.59	0.83
				ConFor_w	13.31	0.57	
				BankProt	0.35	0.18	
				Bars	3.00	0.11	
Calopteryx virgo	108	5.04	0.056	RipVeg	0.35	0.56	0.59
				F020U200	0.76	0.25	
				Crop_w	7.86	0.16	
Leuctra geniculata	108	**7.56**	**0.305**	Urb_w	8.21	0.73	0.84
				BankEro	1.20	0.34	
				Ext_n	25.00	0.24	
				FeatBank	1.75	0.15	
Dinocras cephalotes	108	5.45	0.049	Landuse	0.35	0.37	0.6
				FlowDiv	0.80	0.33	
				Crop_n	3.63	0.20	
				BankEro	3.30	0.06	
Perla marginata	110	5.44	0.133	DecFor_n	13.62	0.28	0.66
				MWD	0.60	0.22	
				RipVeg	1.75	0.22	
				Infrastr	2.45	0.07	
				LocSit	0.35	0.04	
Silo pallipes	109	3.65	-0.009	DecFor_n	13.62	0.13	0.40
				Crop_n	1.21	0.09	
				Ext_n	40.00	0.08	
Silo piceus	110	**7.34**	0.285	ConFor_n	9.39	0.66	0.82
				CrSecFor	0.60	0.52	
				Landuse	1.75	0.20	
				LocSit	0.40	0.05	
Hydropsyche dinarica	94	4.89	0.003	DecFor_w	1.87	1.20	0.67
				DecFor_n	7.43	0.37	
				Ext_n	55.00	0.08	
Hydropsyche incognita	112	3.81	0.173	Erosion	0.25	0.00	0.90
				BankProt	0.35	0.01	
Hydropsyche instabilis	112	5.42	0.164	RipVeg	0.35	0.82	0.74
				DecFor_w	9.69	0.37	
				BankProt	2.45	0.13	
				ConFor_w	53.26	0.07	
				Planform	3.00	0.07	

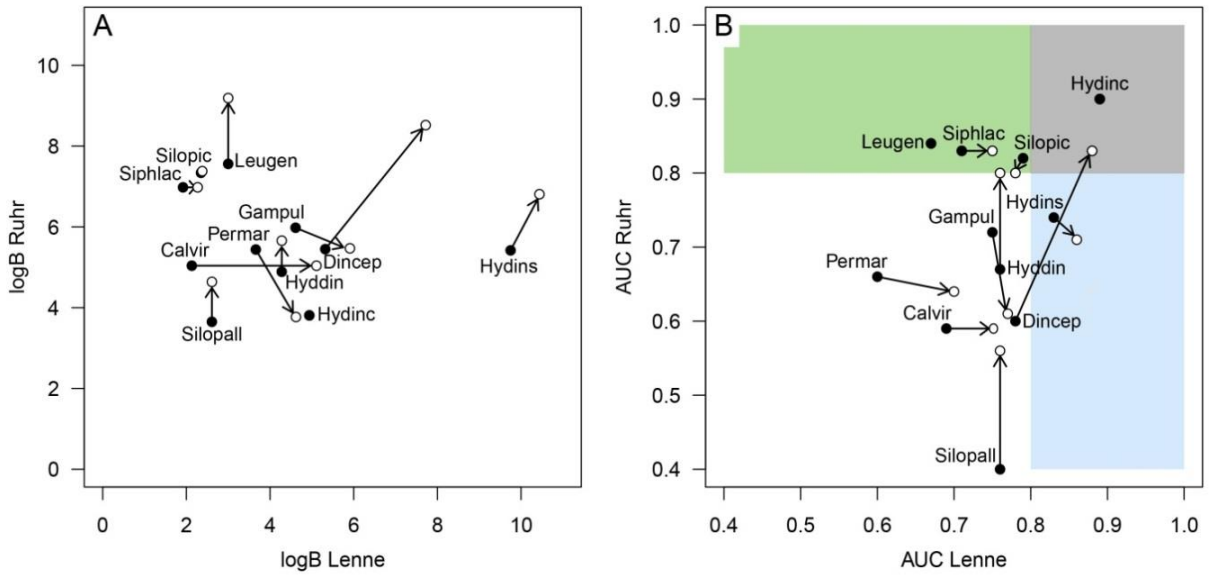

Figure 4.8: Scatterplots of (A) logB values and (B) cross-validated AUC values per watershed. The black points show the logB and AUC values resulting from the SDMs based on broad-scale variables, the white points show logB and AUC values resulting from SDMs based on broad-scale and local variables (physic-chemistry and substrates). The arrows show the direction of change. Positive gain in SDM performance is indicated by arrows pointing towards the upper part, the right part or the upper right corner of the plots. In B: shaped areas indicate the interval of AUC values 0.8-1.0 defining good predictive performance according to Araújo et al. (2005) of the Lenne (blue) and Ruhr (green) watersheds.

Concerning broad-scale models, SDMs of the Lenne watershed more often included in-stream physical habitat features (e.g. longitudinal bars, riffles or substrate diversity), while bank and riparian features were more often found in SDMs of the Ruhr watershed (Figure 4.9). Watershed-specific differences in predictor sensitivity were also found for land use. Extensive land use like pasture and grassland were more sensitive in the Lenne models than in the Ruhr models. Notably, however, a stronger gradient of extensive land use was found for the sites in the Ruhr watershed (Appendix 2a E+F). Percent forested area revealed a stronger influence in the Lenne models, too (Figure 4.9). Unexpectedly, intensive land uses (cropland, urban area) had only a moderate influence on the models.

When local predictors were included into the models, a shift in sensitivities from broad-scale to local predictors was obvious in both watersheds. Importance of channel bank and riparian features as well as forested areas in the Lenne models decreased due to strongly increased sensitivities of physico-chemical and substrates parameters. In the Ruhr models, physico-chemical predictors had the highest mean influence, while in-stream predictors (channel bed features and substrates) and intensive land use showed decreasing sensitivities compared to the initial broad-scale models.

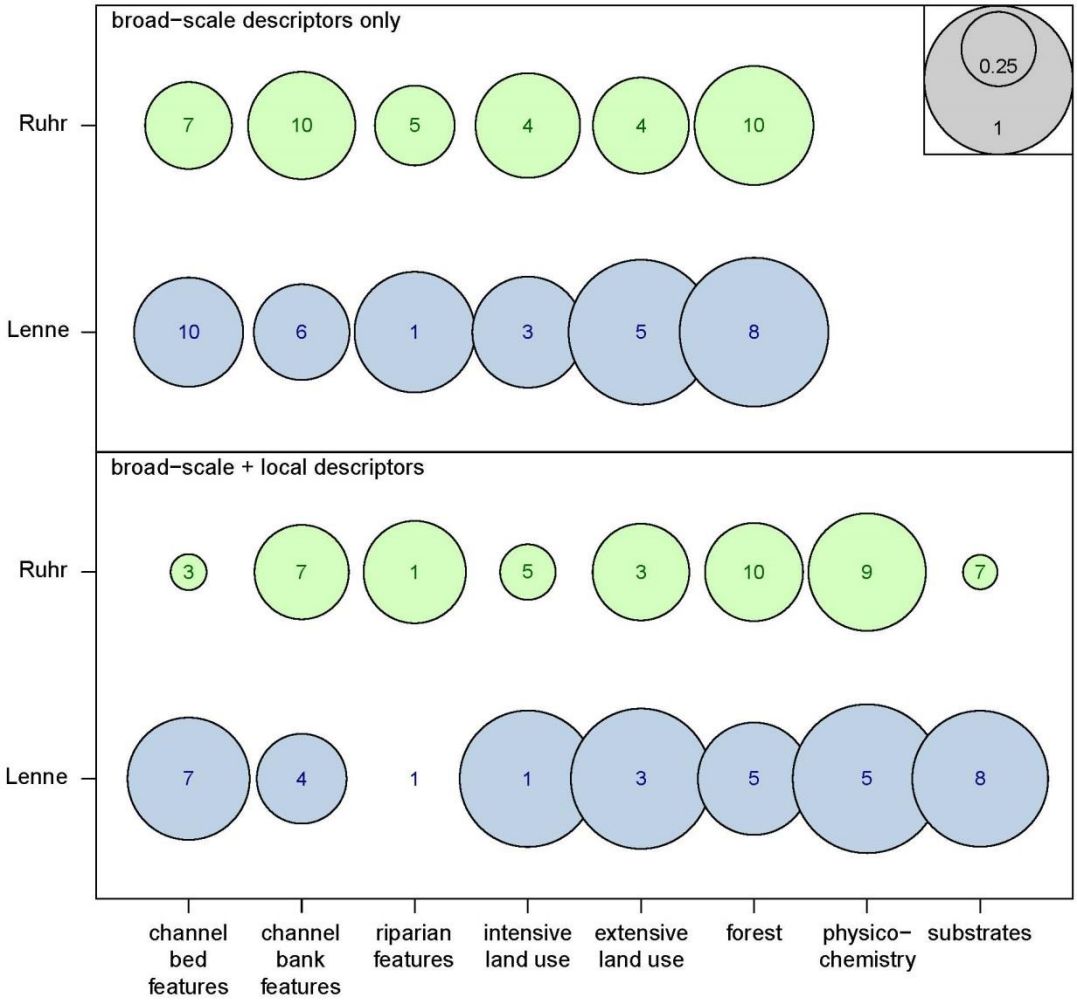

Figure 4.9: Influence of predictor sets per watershed in broad-scale models (A) and models including additional local predictors (B). The bubble size indicates the importance of the variable groups (measured as mean sensitivity) in the distribution models of either watershed. The number in the bubble center indicates the number of predictor variables included into the respective models.

4.3.3 Transferability of models across watersheds

Model transferability between watersheds was tested for six species showing acceptable model fits (*L. geniculata, S. piceus* and *S. lacustris* in Ruhr watershed, *H. instabilis* and *D. cephalotes* in Lenne watershed) or high discriminative performance (*H. incognita*). Species prevalences in both watersheds were tested for comparability using the Chi^2 test. Generally, transferability was low throughout all models with TI values ranging 0.37–0.57. The highest transferability was found for *D. cephalotes* and *S. lacustris* (Figure 4.10), whereas TIs were much lower for those species that performed best in both watersheds (Lenne: *H. instabilis*; Ruhr: *L. geniculata*). The lowest transferability was found for *H. incognita*, while TI was incalculable for *S. piceus* because of high amounts of missing predictions of Ruhr models to the Lenne watershed that were due to a smaller neighborhood size than defined as minimum (25% of the average neighborhood size).

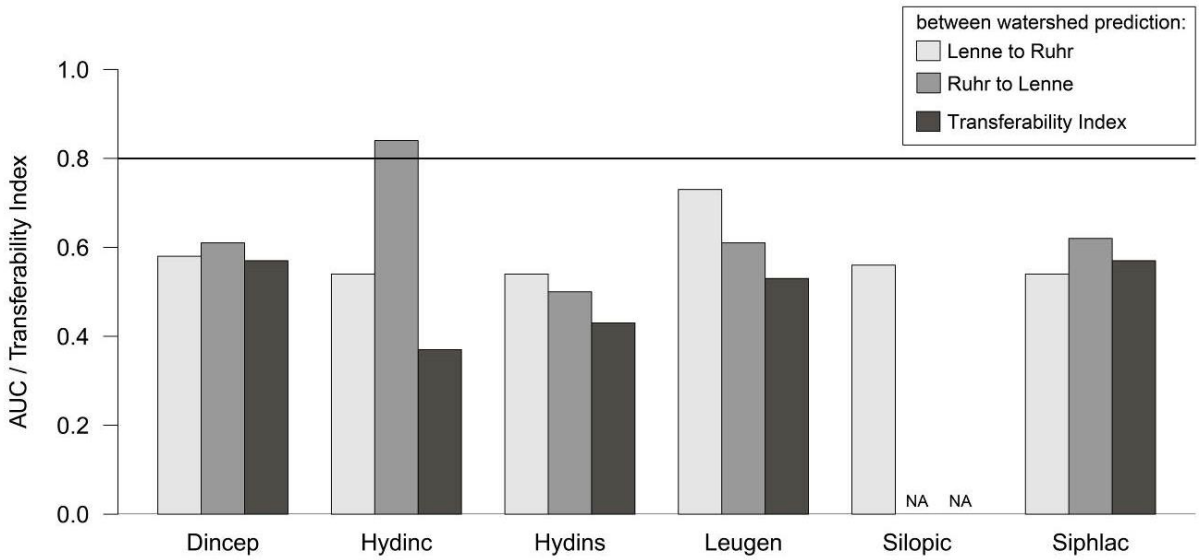

Figure 4.10: Predictive power (AUC) of between-watershed prediction (light and medium grey bars) and Transferability Index (dark grey bars). Horizontal line indicates good to perfect predictive power / transferability (AUC/TI = 0.80-1.00) between watersheds according to Araújo et al. (2005).

The models were projected to the adjacent watershed and comparing those external predictions to internal ones. By a detailed look on internal and external prediction maps, individual SDM predictions were found to be transferable at the scale of smaller river sections, i.e. *D. cephalotes*, respectively (Figure 4.11). Some species observations are located to sections which are predicted to exhibit intermediate probabilities of occurrences. Concordance of within- and between-watershed prediction of both watersheds revealed high amounts of mismatches (48–88%), especially for absence sites. Concordance for presence sites was much lower (<5%, Appendix 2e).

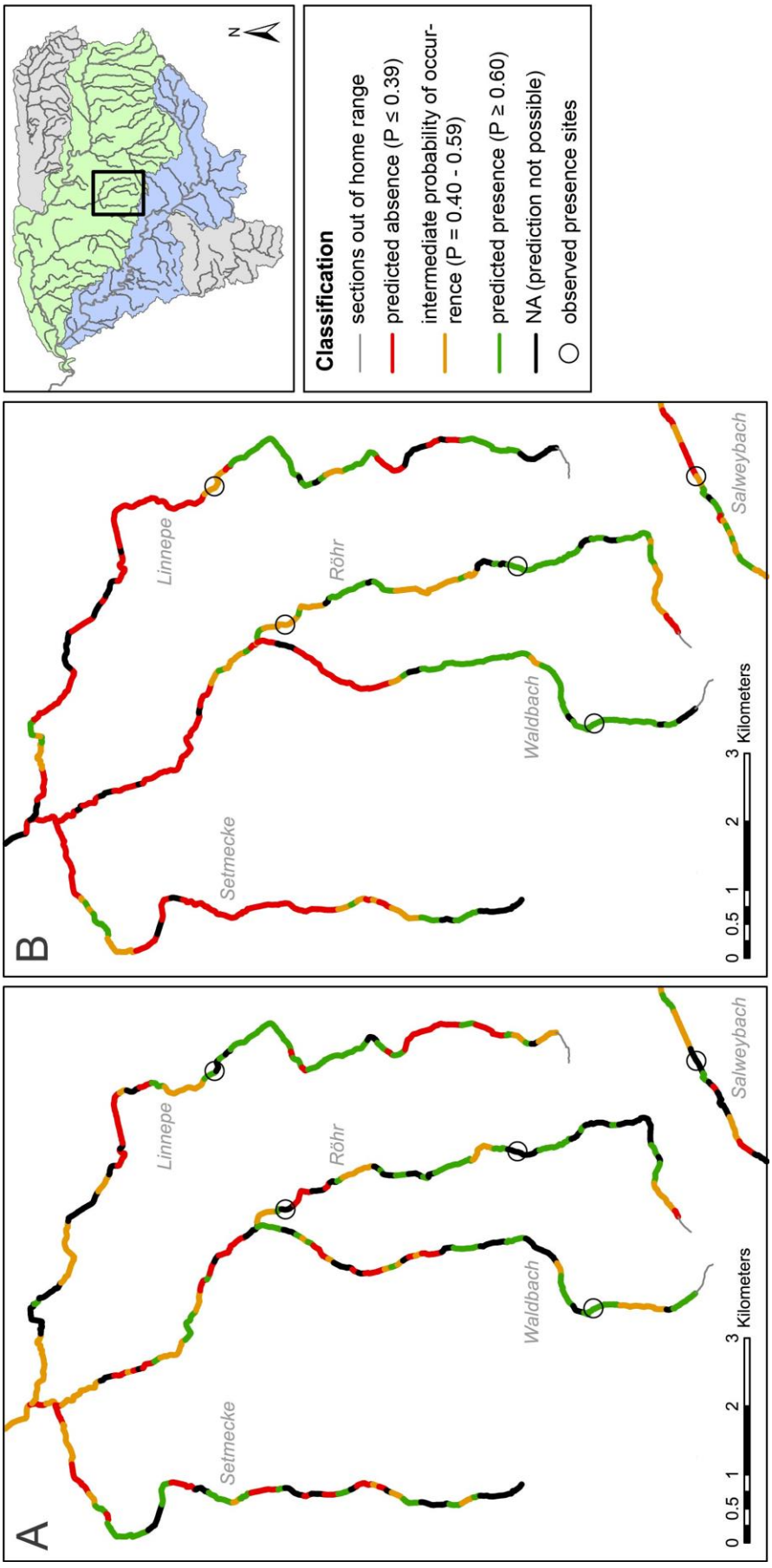

Figure 4.11: Example of a predictive map of *Dinocras cephalotes* with prediction outcome of Ruhr SDMs applied to Ruhr watershed (A, internal evaluation) and prediction outcome of Lenne SDMs applied to Ruhr watershed (B, external evaluation).

4.4 Discussion

4.4.1 Broad- and fine-scale predictors in SDMs

Overall, the SDM's performances were modest, with comparable model fits indicated by logB and xR^2 values. The surrogate character of the predictor variables used in this study may be responsible for this finding. Aquatic stages of benthic invertebrates depend on habitat conditions at scales of centimeters: presence of substrates of certain grain sizes (e.g. for biofilm development for grazers or hiding places under stones or in fine sediments), oxygen concentration directly above or beneath stones or current velocities in a distance of a few millimeters above the substrate. Terrestrial stages depend on microclimatic conditions or light patterns in the riparian vegetation, which are needed for species-specific swarming or mating behavior. These fine-scale conditions of direct relevance to the species can hardly be modeled at a watershed scale. The data resolution used here may not cover the entire variation of each species' habitat although all observed microhabitats and local key factors like water temperature and oxygen content within the sites were recorded. Thus, this variability across watersheds can only be attenuated to some extent. Additionally, these fine-scale variables are mostly insufficiently distributed across watersheds and thus, can hardly serve as predictor variables if watershed-wide prediction is needed. Hence, broad-scale physical habitat conditions (e.g. the presence of bed and bank modifications at the scale of 100 m sections) and riparian land use are therefore habitat proxies rather than ultimate habitat variables for benthic invertebrates. For example, bed and bank enforcement may be linked to a decrease in substrate and overall habitat diversity, but cannot account for the presence or absence of habitats ultimately required by a species to fulfill its life cycle. Species response patterns to proximate environmental gradients thus depend on the nature of its correlations with the ultimate habitat conditions (Franklin et al. 2000, Guisan & Zimmermann 2000). Yet, although the latter may lead to more robust models, the ultimate habitat conditions are often difficult to determine and record and thus, least practical in forecasting species distribution at the broad scale (Austin 2002).

Moreover, streams are strongly heterogeneous ecosystems comprising highly dynamic processes within the catchment and site scale that shape the distribution of species via the connectivity of the stream network and the lateral and vertical linkages to terrestrial and groundwater interfaces (Domisch et al. 2015). This makes it hard to consider all relevant factors that directly or indirectly affect species occurrence.

Several SDM studies have implemented catchment characteristics and land use as model predictors for fish species (e.g. Leathwick et al. 2006, Lohse et al. 2008). Riparian land use was detected to have significant influence on benthic macroinvertebrates (Allan 2004, Death & Collier 2010, Feld 2012, Lorenz & Feld 2013). Due to that, I also included broad-scale

riparian land use and found nearly all models selecting riparian land use categories as predictors for species distributions, indicating the importance of riparian characteristics instead of the sole use of in-stream features. The rationale behind this linkage can either be based on in-stream conditions, which are shaped by riparian vegetation (water temperature, macrophyte growth, or supply of particular organic matter (POM) as food for shredders among the invertebrates) or directly on the riparian vegetation as a habitat of adult aquatic insects.

Guisan & Zimmermann (2000) stated that in many cases the implementation of indirect gradients is useful because they usually replace a combination of different resources and direct correlations. In this study, model performances and predictive power were acceptable for five out of eleven macroinvertebrate species indicating that species distribution modelling is feasible using broad-scale predictor variables.

In general, the sole use of indirect variables instead of directly measured local predictors such as physico-chemistry or substrates may reduce model performance (Segurado & Araújo 2004, Shrestha et al. 2012) as well as transferability to other regions (Randin et al. 2006, Vanreusel et al. 2007, Zanini et al. 2009). Franklin (2009) recommended the implementation of SDMs using both broad-scale and fine-scale predictors. SDMs relying on broad-scale predictors only (e.g. climate) may produce only rough approximations of species' responses and thus, species' distributions. Hence, SDMs based only on surrogate predictors are expected to show less correlative species-environmental relationships than those models including direct predictors. Using limited information on substrate and physico-chemical conditions additionally to continuous broad-scale variables at each site, I was able to examine the effect of including local environmental conditions on model performance and predictive capacity of SDMs. For most species, at least one fine-scale predictor was implemented in at least one out of the two models (except *C. virgo* and *H. incognita*). Several model fits increased when using physico-chemical parameters and river bottom substrates in addition to hydromorphological and land use variables (*C. virgo, D. cephalotes, H. dinarica, H. instabilis, S. pallipes*). In contrast, for other species (*G. pulex, H. incognita, L. geniculata, S. piceus*) no improvement or even a decrease in model fit was found when using fine-scale variables in addition. First, species that gained improved model performance revealed weak models without fine-scale predictors. For these species, fine-scale predictors seem to be of higher importance than in SDMs of species with acceptable model performance (except *D. cephalotes*). Second, *G. pulex, H. incognita* and *L. geniculata* are species widely distributed along the river continuum (see Appendix 2d), while *D. cephalotes*, *H. dinarica* and *S. pallipes* are more closely linked to upstream reaches. This may explain why *D. cephalotes, H. dinarica* and *S. pallipes* better respond to fine-scale variables (especially physico-chemical variables like conductivity and nitrate content), as differences in their occurrences depend stronger on local conditions. Although I suggested the species' preferred distribution along the river continuum to cause different response on fine-

scale variables, this pattern was not consistently obvious (compare *C. virgo* and *S. piceus*). From this point, I can only partly agree with Austin et al. (2006) that fine-scale habitat variables may constitute important predictors of species' distributions at the watershed scale. Direct environmental variables are important predictors which may improve model performance at a certain rate, but the results also support the opposite, i.e. SDM fits may decrease when using fine scale variables. Consequently, the correlative relationship between environmental broad-scale variables and local variables as well as biological data and thus the ability of broad-scale variables to act as proxies for conditions directly affecting macroinvertebrate distributions has to be understood and proven appropriate before the construction of SDMs.

4.4.2 Influence of species prevalence on SDM performance

Species-specific differences in a model's predictive performance are linked to the species' prevalence in the dataset that is known to have an effect on predictive performance (Manel et al. 2001, Stockwell & Peterson 2002, Brotons et al. 2004, Segurado & Araújo 2004). For example, a prevalence of 10% means that a species was recorded present at 10% of the sampled sites, while it was absent at 90%. Consequently, it is much more likely to correctly predict a species' absence than its presence (Fielding & Bell 1997). Predictive performance may appear high even when there is poor correlation between predicted species occurrence and environmental predictors. Species prevalences in this study reached 60% (Figure 4.7), but were much lower for some species and lowest for *H. incognita*. This species occurred at 10% of the Lenne and 5% of the Ruhr sites which in part might explain the high AUC and the accordingly low logB values (see also Brotons et al. 2004).

Furthermore, the dataset of species representing a high prevalence is more reliable as a species' record at a site leaves no doubt that the species is occurring. In contrast, if a species was not recorded at a site, it might have been overlooked (type I sampling error). To reduce this error, I conducted a thorough time-based sampling that accounted for multiple replicate samples per habitat (including rare habitats like lentic standing waters at bank sides or emerged roots of terrestrial plants) for altogether 45 minutes at each site. In addition, the subsampling of data aimed at the reduction of the type I sampling error, by excluding river sections that fall out of the realized niche of the species. However, false absences in the dataset cannot be excluded and may still have an influence on the models.

For rare species, presences are usually scarce and higher amounts of absences are accompanied by a high proportion of false absences whose inclusion is a confounding factor interacting with prevalence (Jiménez-Valverde & Lobo 2006). Several authors found that modelling distributions of species with restricted range sizes and lower frequencies (specialists) are modelled with a higher accuracy than that of common species and generalists

(Stockwell & Peterson 2002; Segurado & Araujo 2004; Tsoar et al. 2007; Lobo et al. 2008; 2010). However, low prevalence is usually a property of data from specialist and/or endangered species that are typically in focus of ecology and conservation management (Jiménez-Valverde & Lobo 2006).

According to McPherson et al. (2004) prevalences around 50% facilitate the highest AUC values. Liu et al. (2005) suggested to use response data with medium prevalences of 50% because most predictive performance measures are depending on species prevalence within the model training data set. Providing response data equally distributed in presences and absences is often not viable in ecological research because of very variable prevalences, especially when presence-only data are available for rare and endangered species that are in the focus of conservational research.

4.4.3 Transferability across watersheds

Transferability of species distribution models from one area to another can help reduce the usage of resources for continuous field monitoring. For instance, referring to this study, it might be sufficient to set up a model once for a representative watershed and then apply this model in adjacent watersheds characterized by comparable environmental conditions.

It was already shown that the Lenne and upper Ruhr watersheds are similar according to the species pool and most single broad-scale variables, but they slightly differed concerning the overall environmental gradients. Due to the fact that the study watersheds adjoin directly to each other, macroinvertebrate distribution models were expected to show similar results in model performance and predictive power and thus, being spatially transferable between either watersheds.

However, the transferability index (TI) revealed no transferability for most macroinvertebrate SDMs based on my data. A few species showed an asymmetrical transferability, i.e. an unidirectional transferability from one watershed to another but not vice versa. Randin et al. (2006) and Barbosa et al. (2009) explained this ‘partial transferability’ with regional (land use history, microclimate) and biological factors (abundance, interactions, functional traits). Among these, legacy land use and water pollution might prevail also in this study. Though industrial waste water is treated nowadays and does not affect water quality, legacy pollution effects species occurrences by heavy metals or different land coverage. Legacies of historic land use were found to affect the present invertebrate species diversity in streams. This indicates that large-scale and long-term agricultural disturbances in a watershed may limit the recovery of stream diversity for many decades (Harding et al. 1998). According to this, the lack of recolonisation processes may have eradicated macroinvertebrate populations over a long time

(see Sondermann et al. (2015) for a study of modelling dispersal and recolonisation of stream sections by macroinvertebrate species). These differences in land use history and thus, overall environmental conditions may help understand the different distribution patterns across both watersheds.

The indirect (proximate) nature of environmental variables is also likely to partially explain the watershed-specific results. Although land use and physical habitat structure were similar between the Lenne and upper Ruhr, I suggest that their watersheds differ in relation to additional ultimate, but unknown habitat parameters. For example, agricultural land use in the riparian zone is often linked with nutrient and fine sediment pollution (Allan 2004; Feld 2012), which in turn alters fine-scale riverine habitat conditions. The correlation between proximate (broad-scale) and ultimate (fine-scale) variables may be different even in adjacent watersheds, for instance because of different land use histories and thus, have different implications on fine-scale habitat conditions. Similarly, physical habitat alteration constitutes a diverse impact family, so that the same kind of broad-scale habitat alteration does not always translate into the same habitat impacts at the fine-scale. Furthermore, the relationship between a response variable and an indirect predictor variable are expected to change with region and (or) time, while the relationship between a response variable and a direct predictor variable are expected to change less (Sundblad et al. 2009).

Moreover, SDMs represent static records as they consider actual observations of one species but mostly exclude the time dimension. Consequently, dispersion through time and space of individual species is not considered in this modelling approach, although dispersal is known to be an important factor in macroinvertebrate ecology, as species-specific dispersal capacity determines mobility, competitive ability and (breeding) habitat selection. An integrative implementation of distribution models that are linked to the species mobility (as presented by Sondermann et al. 2015), hydrologic and hydraulic dynamic processes in rivers (see Kiesel et al. (2009) for an integrative abiotic modelling approach) and multiple scales incorporating both catchment and site scale based predictors (see also Domisch et al. 2015) are future applications of SDMs that may provide reliable, informative and easily applicable tools in river assessment and conservation management.

5 Influence of different validation approaches and species prevalence on the predictive performance of broad-scale distribution models

---

Parts of this chapter are published in Hydrobiologia.

Reference:

Gies, M., Sondermann, M., Hering, D. & Feld, C.K. A comparison of modelled and actual distributions of benthic macroinvertebrates in a Central European mountain catchment. Hydrobiologia, online first.

5.1 Introduction

Species distribution models (SDM) constitute an important tool in applied ecology, biogeography and conservation and risk management of terrestrial and aquatic ecosystems, capable of identifying species' habitat requirements in a descriptive way. The usefulness of a SDM is ultimately judged on the *model performance* (synonyme to goodness-of-fit) which results from a *model training* process to obtain the best model for the focal species. Model performance is expressed by a variety of measures dependent on the SDM method used (see Box 1 for a glossary).

One step further predictive models are implemented to estimate species occurrences based on a set of environmental predictors. Especially when predictions are made to independent regions (e.g. Olden & Jackson 2000; 2002, Elith et al. 2006) or times (e.g. Buisson & Grenouillet 2009, Domisch et al. 2013a) with unsampled locations, the model's ability to fit with real species occurrences has to be thoroughly tested against real species data, e.g. training or independent data (Araújo & Guisan 2006), a process called *model validation* (Rykiel 1996, Mouton et al. 2010, Eskildsen et al. 2013, Box 1). The majority of studies using SDMs to project species distributions use a simple form of validation (a combined resubstituition approach) in which the same data used for model training are consulted also to validate the models (Araújo et al., 2005, Araújo & Guisan 2006). *Cross-validation* is based on the repeated split of data into subsets for training and validation (Power 1993, Osborne & Suárez-Seoane 2002, Bahn & McGill 2013). In each split, a training dataset is used to develop the SDM, and the validation subset is then used to test the predictions of the modeled species' presence/absence. Bootstrap methods can be added for significance testing of the validation (Kohavi 1995, Hastie et al. 2001, Hirzel et al. 2006). The shortcoming of this cross-validation is its use of spatially autocorrelated data for training and validation (Araújo et al. 2005). This can be overcome by the usage of independent observations out of regular field surveys or monitoring to validate a SDM (*independent validation*). Spatio-temporal independence can be achieved, for instance, with data from a different region or sampled at a different time (Araújo & Guisan 2006, Randin et al. 2006). To my knowledge, however, the latter is rarely applied in SDM (e.g. Mladenoff et al. 1999).

Ideally, SDMs are based on direct environmental predictors, i.e. predictors that directly determine habitat suitability of the targeted species, and determinants at the catchment scale. The spatial scale of predictors hence is dependent on the habitat range of a species. For riverine benthic macroinvertebrates, this is a rather fine spatial scale (square centimeters up to hundreds of square meters for most species, e.g. related to the preferred substrates or local flow conditions), which cannot easily be up-scaled to broader spatial scales. Fine-scale habitat data are usually not available for entire catchments or larger regions. Instead, broad-scale

SDMs use proxy variables, i.e. predictors that are indirectly related to a species habitat like water quality, land use (Allan 2004, Feld 2012) and morphology (Kail & Hering 2009) in the upstream reaches. SDMs using broad-scale predictors are commonly linked to scenarios and projections of species distributions linked to shifts caused by changing climate, extinction risk (e.g. Araújo et al. 2005, Thuiller et al. 2005a, Buisson & Grenouillet 2009, Domisch et al. 2013a) or species invasions (e.g. Peterson 2003, Thuiller et al. 2005b, Evangelista et al. 2008).

The frequency of species occurrences (species prevalence) is known to affect predictive performance as a statistical artefact, especially when it is extremely low or high (Fielding & Bell 1997, Pearce & Ferrier 2000) but it is also essential for the assessment of model calibration (Lawson et al. 2014). Rare species with (extremely) low prevalence are commonly subject to conservation management and thus to SDM studies. Hence, besides its goodness-of-fit and *predictive performance* the influence of a species' prevalence on the overall SDM performance should also be considered.

In this study, SDMs on eleven aquatic insect species were developed based on the data collection 2010. Broad-scale (proxy) environmental predictors (e.g. physical habitat quality, upstream riparian land use) were used to predict the species' distributions. I investigated model and predictive performances of SDMs using two regression methods (binary logistic regression and non-parametric multiplicative regression). Besides standard cross- and independent validation procedures, I also introduce a *field validation* approach comparing SDM predictions to field data that were additionally sampled after macroinvertebrate species occurrences were projected within river watersheds. I anticipated that field validation, as a direct verification of SDM prediction, would give a more realistic view of an SDM's predictive performance. As the problem of spatial autocorrelation is not overridden by carrying out additional field sampling within the same region as the model was trained for (Araújo & Guisan 2006), the range of the additional sampling sites was extended to watersheds beyond.

The aims were i) to compare model and predictive performance results, ii) to compare the results of different validation methods and iii) to quantify the role of species prevalence in the predictions of SDMs on benthic invertebrates.

Box 1 Glossar of specific SDM terms (marked in italics)	
Term	**Description**
Model training	Setting up a model using specific SDM methods, calibration and selection of the best performing model, see *model performance*.
Model validation	Comparison of SDM predictions to actual species observations to judge on a model's *predictive performance*, also referred to as model evaluation (Barbosa et al. 2013, Barry & Elith 2006)
Model performance	Refers to the goodness-of-fit of a model giving the strength of the relationship between species and environmental variables. Examples of model performance measures are coefficients of determination (R^2) and the Log likehood ratio (logB) in NPMR models.
Predictive performance	Refers to the SDM's ability to correctly predict spatial species occurrences, e.g. the matching of SDM's predictions to real species occurrences. To judge on the predictive performance several measures have been developed. The standard threshold-independent measure is the area under the curve (AUC) resulting from the Receiver Operating Characteristics (ROC) analysis which expresses the discriminatory ability of SDMs, i.e. for the ability of a model to correctly distinguish between sites where a species is present versus those where it is absent (Hanley & McNeil 1982, Vaughan & Ormerod 2005). Threshold-dependent measures (e.g. PCC, TSS, TN, TP) are based on the partitioning of the continuous predictions at a certain threshold to allow the comparison to the binary observations.
Cross-validation	Internal validation using the initial species observations to assess predictive performance of a model. Repeated splits of the data into subsets for training and testing (validation) are commonly made automatically (Power 1993, Osborne & Suárez-Seoane 2002, Bahn & McGill 2013). In each split, a training dataset is used to develop the SDM, and the validation subset is then used to test the predictions of the modeled species' presence/absence. Cross-validation is therefore commonly based on resubstitution.
Independent validation	External validation using independently sampled species data, e.g. survey data of a monitoring programme or historical data. The term is sometimes used for validation via data separation beforehand (for instance, a 70/30% split). Thus, one data set is used for model training and the other for model validation.
Field validation	External validation using new observation data out of a second field campaign. The SDM predictions were directly verified in the field at river sections selected beforehand.

5.2 Materials and Methods

5.2.1 Data base

The presence and absence of eleven benthic macroinvertebrate species (Table 5.1) was recorded at 225 sampling sites (ca. 100 m long sections) during two field campaigns in spring 2010 (121 sites) and 2011 (104 sites), see Figure 5.1 for an overview of the sampling sites. Species data of the year 2010 were used to train the models and to project species occurrences along the river courses within the entire study catchment. In 2010, site selection was random, but topologically stratified to ensure a representative coverage of the dominant river types of the model catchment. In 2011, random site selection was additionally stratified according to the predicted presences and absences based on SDMs on the 2010 data. This ensured a balanced coverage of predicted presences and absences of model species in the final validation data set. At each sample site, all habitats were thoroughly inspected in order to reduce the record of false absence, i.e. overlooked species.

Table 5.1: Eleven model species and their prevalence in both sample campaigns (216 sampling sites in total, 112 in 2010 and 104 in 2011).

Order	**Species**	**Prevalence (%)**		
		2010	**2011**	**2010+2011**
Amphipoda	*Gammarus pulex* (LINNAEUS, 1758)	45.5	28.8	37.8
Ephemeroptera	*Siphlonurus lacustris* (EATON, 1870)	15.7	31.7	23.1
Odonata	*Calopteryx virgo* (LINNAEUS, 1758)	20.7	26.9	23.6
Plecoptera	*Leuctra geniculata* (STEPHENS, 1836)	24.0	25.0	24.4
	Dinocras cephalotes (CURTIS, 1827)	26.4	42.3	33.8
	Perla marginata (PANZER, 1799)	33.1	44.2	38.2
Trichoptera	*Silo pallipes* (FABRICIUS, 1781)	32.2	32.7	32.4
	Silo piceus (BRAUER, 1857)	27.3	15.4	21.8
	Hydropsyche dinarica MARINKOVIC, 1979	19.0	26.0	22.2
	Hydropsyche incognita PITSCH, 1993	8.3	6.7	7.6
	Hydropsyche instabilis (CURTIS, 1834)	49.6	55.8	52.4

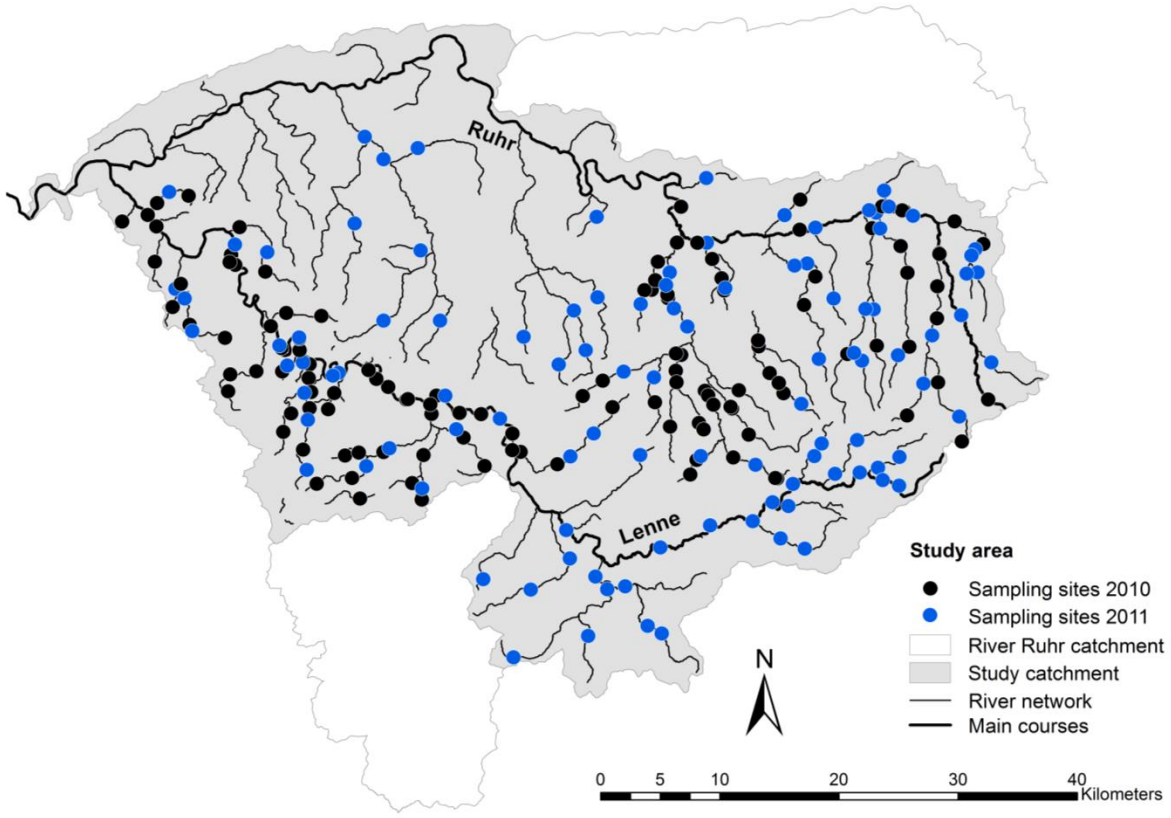

Figure 5.1: Sample sites of the years 2010 (training data, black points) and 2011 (validation data, blue points) within the study area.

Hydromorphological habitat quality and land use as environmental descriptors were used in the SDMs (see chapter 2.4). Physical habitat quality was based on the German hydromorphological survey (Kail & Hering 2005) that provides a classification based on the assessment of 25 single hydromorphological parameters (resolution: 100 m sections of the entire river network) (see Table 5.2 for a list of hydromorphological and land use parameters used here). Land use data derived from the ATKIS land cover survey (ATKIS 2007, spatial resolution: 5 m) covered five categories in two riparian buffer widths (20 m (narrow) and 200 m (wide) within 1 km upstream reach. Finally, distance to source (m) and altitude a.s.l. (m) of the upstream edge of each sample site were used as proxies of stream size and related water temperature, to account for the natural variability inherent to the data. This resulted in 32 environmental predictor variables for 216 out of 225 sampling sites (104 in 2010 and 112 in 2011). Due to missing values in the data input matrix 9 sampling sites had to be excluded from further modelling. Colinearity of the variables was tested using Spearman rank correlation coefficients and a variance inflation factor analysis (VIF) that showed no colinearity between land use variables and physical habitat quality (Table 4.3). The wide applicability of predictor variables in the entire watershed enabled predictions for a total of 10,701 100 m sections.

Table 5.2: Broad-scale environmental parameters on topography, physical habitat quality and riparian land use that were included into all model approaches. Hydromorphological survey data provided 25 categorical parameters in total of which 15 were selected as appropriate for modelling due to their environmental gradients within the data set 2010. Land use categories were derived from ATKIS land cover data (ATKIS 2007) available as percentage of coverage.

	Environmental parameters		**Abbreviation**
Natural	altitude a.s.l. (m)		altitude
	distance to source (m)		source_m
Channel bed features	Planform		Planform
	Erosion at bends		Erosion
	Features indicating natural channel dynamics (e.g. wood jams, island, widening)		FeatDyn
	Riffles and steps		Riffles
	Flow diversity		FlowDiv
	Substrate diversity		SubsDiv
	Channel features (e.g. scour- and backwater pools, rapids, cascades)		FeatChan
Channel bank features	Bank erosion (indicating widening of channel)		BankEro
	Riparian vegetation		RipVeg
	Bank protection		BankProt
	Bank features (e.g. woody debris, undercut banks)		FeatBank
Floodplain	Land-use		Landuse
	Riparian buffer strip		RipBuff
	Infrastructure works (e.g. roads, dumping sites, fish-farms)		Infrastruc
	Local situation (urban/landscape)		LocSit
Land use categories by ATKIS	Cropland (%)	10 m on either bank side (narrow)	Crop_n
		100 m on either bank side (wide)	Crop_w
	Extensive/pasture (%)	10 m on either bank side (narrow)	Ext_n
		100 m on either bank side (wide)	Ext_w
	Deciduous forest (%)	10 m on either bank side (narrow)	DecFor_n
		100 m on either bank side (wide)	DecFor_w
	Coniferous/mixed forest (%)	10 m on either bank side (narrow)	ConFor_n
		100 m on either bank side (wide)	ConFor_w
	Urban/industrial area (%)	10 m on either bank side (narrow)	Urb_n
		100 m on either bank side (wide)	Urb_w
	Ratio %forest in 200 m buffer / %urban in 20 m buffer		F020U200

5.2.2 Species distribution modelling

SDMs were developed using two methods: nonparametric multiplicative regression (NPMR) and logistic regression (LR).

With binary (presence/absence) response data, NPMR model statistics include a measure of goodness-of-fit (i.e. log10 of the likelihood ratio logB) and a cross-validated coefficient of determination (i.e. pseudo-R^2 or xR^2). The statistical significance of logB was tested using a Chi^2-distribution with one degree of freedom and significance level of 0.05. SDMs revealing the highest logB value were selected as the best models.

Opposed to NPMR, logistic regression was used as a standard regression method in the application of binary species data. The regression coefficients of the selected descriptor variables were tested using a Wald statistic, with values <0.05 indicating useful descriptor variables. To describe a LR model‘s goodness of fit, Nagelkerke's pseudo-R^2 (Nagelkerke 1992), was applied and further tested using the Hosmer-Lemeshow statistics (Hosmer & Lemeshow 2000).

However, xR^2 and Nagelkerke's R^2 are equivalent to a linear R^2 and describe the ratio of explained variance of the model.

Based on these measures, the best SDMs of each method were used to predict the probability of each species’ occurrence within the entire study area. For NPMR prediction, a conservative scenario and an average neighborhood size of 1 were used. During the prediction procedure, NPMR assigns a missing value instead of an estimate of probability if the neighborhood size of this sampling point is smaller than the criterion minimum. Prediction maps were then generated in ArcGIS 10 (ESRI 2011).

5.2.3 Model validation

For model validation, threshold-dependent and threshold-independent measures were applied. Threshold-dependent measures require the definition of a threshold (or split point) for the prediction value, at which presence and absence are distinguished. It is usually set to 0.5 (e.g. Manel et al. 1999b, Manel et al. 2001, Stockwell & Peterson 2002), as used also above for prediction mapping, with values below 0.5 interpreted as absence and values above interpreted as presence of a species. The threshold is also required to develop a confusion matrix (Table 2.6) contrasting correctly (true) and incorrectly classified (false) presences and absences for an individual model species (Fielding & Bell 1997). The threshold-dependent performance of the models is measured using the precentages of true positives and true negatives, the overall accuracy described as the percentage of correctly classified observations (PCC) and the true skill statistic (TSS). PCC includes both the proportion of true

positives and negatives (i.e. TP + TN, Fielding & Bell 1997, Stockwell & Peterson 2002). The TSS (Allouche et al. 2006) takes into account both omission and commission errors and success as a result of random guessing (i.e. sensitivity + specificity – 1). The TSS is independent of prevalence ranging between 1 (perfect agreement) and -1 (performance no better than random).

For threshold-independent model validation, the area under the curve (AUC) of a receiver operating characteristic function (ROC) for each model (Swets 1988, Elith et al. 2006, Reusser & Lee 2008) was calculated. AUC measures the discriminatory ability for distinguishing between sites where a species is present, versus those where it is absent (Hanley & McNeil 1982, Vaughan & Ormerod 2005). Reliable predictive performance is characterized by a large area under the curve (AUC ≥ 0.80) (e.g. Manel et al. 2001, Araújo et al. 2005, Elith et al. 2006).

Three different validation approaches were conducted. First, the standard cross-validation compares the predictive model output to the initial species data used for model training, applying a resubstitution procedure. Cross-validation in HyperNiche is implemented by a 'leave-one-out cross-validation' procedure (McCune 2006). This is a common procedure in predictive modelling and is based on data resampling, with k – 1 subsamples being used as training data and the remaining subsample as validation data for testing the model (Kohavi 1995). The procedure is repeated k times (k-fold), i.e. each of the k subsamples is left out once and used for validation (Hastie et al. 2001, Arlot & Celisse 2010). With logistic regression, cross-validation was performed manually by comparing a model's prediction with the initial presence/absence data on which the models were built.

In addition to the cross-validation, secondly, a real independent validation was applied using 620 sampling points which were provided by the LANUV NRW monitoring program in the years 2004 – 2009 and former internal sampling campaigns. Sampling data collected in spring seasons were selected to be appropriate validation data. In cases of doubled sampling points during this time period the latest information on species' occurrences were used for validation.

To test whether using additional field data gives more appropriate results on predictive performance, thirdly, an alternative field validation approach was conducted based on two datasets in addition to cross-validation. The alternative validation approach was based on two datasets. The 2010 data were used for model training and the 2011 data for model validation. Again, TSS, PCC and AUC were calculated to estimate the model's predictive quality (hereafter abbreviated fieldTSS, fieldPCC and fieldAUC) and were compared to the output of a cross-validation (hereafter abbreviated crossTSS, crossPCC and crossAUC) and independent validation procedure (hereafter abbreviated indTSS, indPCC and indAUC). The conceptual approach of modelling and validation is given in Figure 5.2.

All confusion matrices, model performance statistics, AUC values and related ROC curves were computed using the packages 'PresenceAbsence' (Freeman & Moisen 2008) and 'ROCR' (Sing et al. 2009) in R 2.14.2 (R Development Core Team 2012). Correlations between cross- and field-validated performance measures and species prevalence were calculated using Pearson's correlation coefficient, followed by a Student's t-test to determine significance (normality tested with a Shapiro-Wilk test).

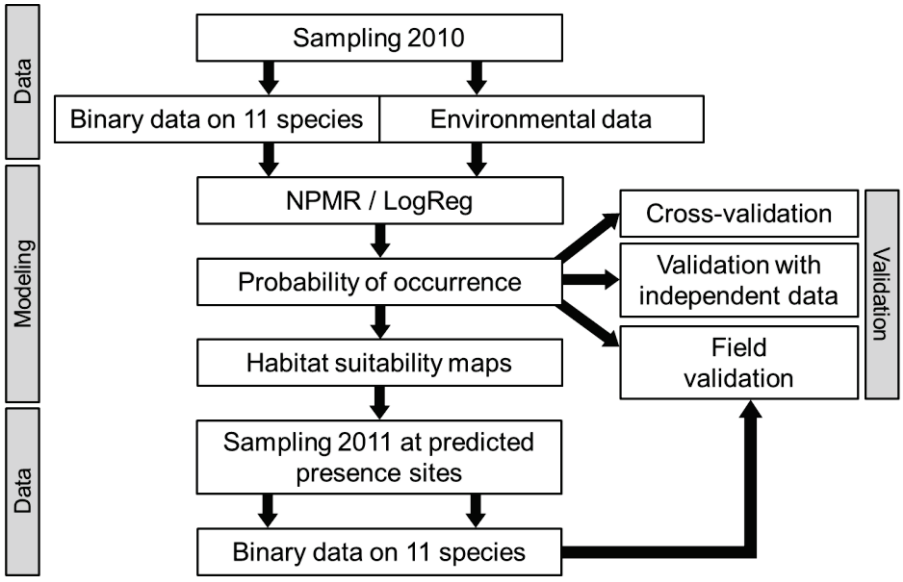

Figure 5.2: Conceptual analytical approach of this study.

5.3 Results

In general, and irrespective of the regression method, the SDMs reached a moderate to poor goodness-of-fit, with pseudo-R^2 values around 0.50 or smaller (Table 5.3). Except for the models of *Silo pallipes* and the LR models of *Hydropsyche incognita* and *Silo piceus*, all models were significantly better than a random model. The best models were obtained for *Dinocras cephalotes*, *S. pallipes* and *S. piceus* with pseudo-R^2 values of 0.35/0.36, 0.34/0.50 and 0.45/0.39 of NPMR and LR models, respectively.

All SDMs (NPMR and LR) performed better in the prediction of absences (Figure 5.3) which is known to be related to the prevalence of the species in the dataset (see below). In this study, the prevalence of the taxa ranged between 8.3 and 49.6% (Table 5.1). Differences between both modelling methods were more obvious for predicted presences (Figure 5.3). Predictions of NPMR and LR models were concordant in up to 80% of the 10,701 river sections in the study catchment (e.g. for *D. cephalotes*, *Hydropsyche dinarica* and *S. lacustris*) showing similar distribution patterns. For instance, for *D. cephalotes*, both models presented high

probabilities of occurrences (>0.50) in small tributaries while the species is predicted absent in the main courses of Lenne and Ruhr (Figure 5.3). However, for other species (e.g. *S. pallipes*) predictions of NPMR and LR models strongly differed.

The comparison of the model performance with the validation results showed a concordance of both measures. SDMs with pseudo-R^2 values >0.30 had a good validation performance (*D. cephalotes*, *H. dinarica* and *S. pallipes* in NPMR model, Table 5.3). The validation performance was rather weak for SDMs with pseudo-R^2 values <0.30 (e.g. *Calopteryx virgo*, *Gammarus pulex*, *Perla marginata*).

Despite the weak model fits, the cross-validation procedure revealed acceptable to high AUC values, thus indicating a good discriminatory power of many SDMs. Thereby, those SDMs with pseudo-R^2 values >0.30 also had cross-validated AUC values >0.80 (except the LR model of *S. pallipes*). Yet, in turn high cross-validated AUC values did not necessarily correspond with high pseudo-R^2 values (e.g. the models of *H. incognita* and *Siphlonurus lacustris*). The correlation of both measures was significant for NPMR results (Table 5.4), but not for LR results (Table 5.5). The correlation of crossAUC and crossPCC, fieldAUC and fieldPCC and of indAUC and indPCC revealed a moderate concordance ($r < 0.70$) of both validation quality measures while AUC was highly correlated to TSS for both NPMR and LR (Table 5.4 and Table 5.5).

The comparison of cross-, field and independent validation approaches showed that cross-validated AUC values equaled or exceeded field-validated AUC values for most models (Figure 5.4). The crossAUC ranged from 0.61–0.91 in NPMR models and 0.47-0.80 in LR models. The field validated AUC values ranged from 0.30–0.83 in NPMR models and 0.46–0.78 in LR models. The indAUC ranged from 0.14–0.77 in NPMR models and 0.06–0.74 in LR models and was thus consistently lower than crossAUC and fieldAUC. Overall, the AUC values decreased from cross- to field to independent validation. For instance, for two species, *S. piceus* and *S. lacustris*, cross-validation implied a high predictive accuracy of NPMR and LR, while field and independent validation resulted in random predictions.

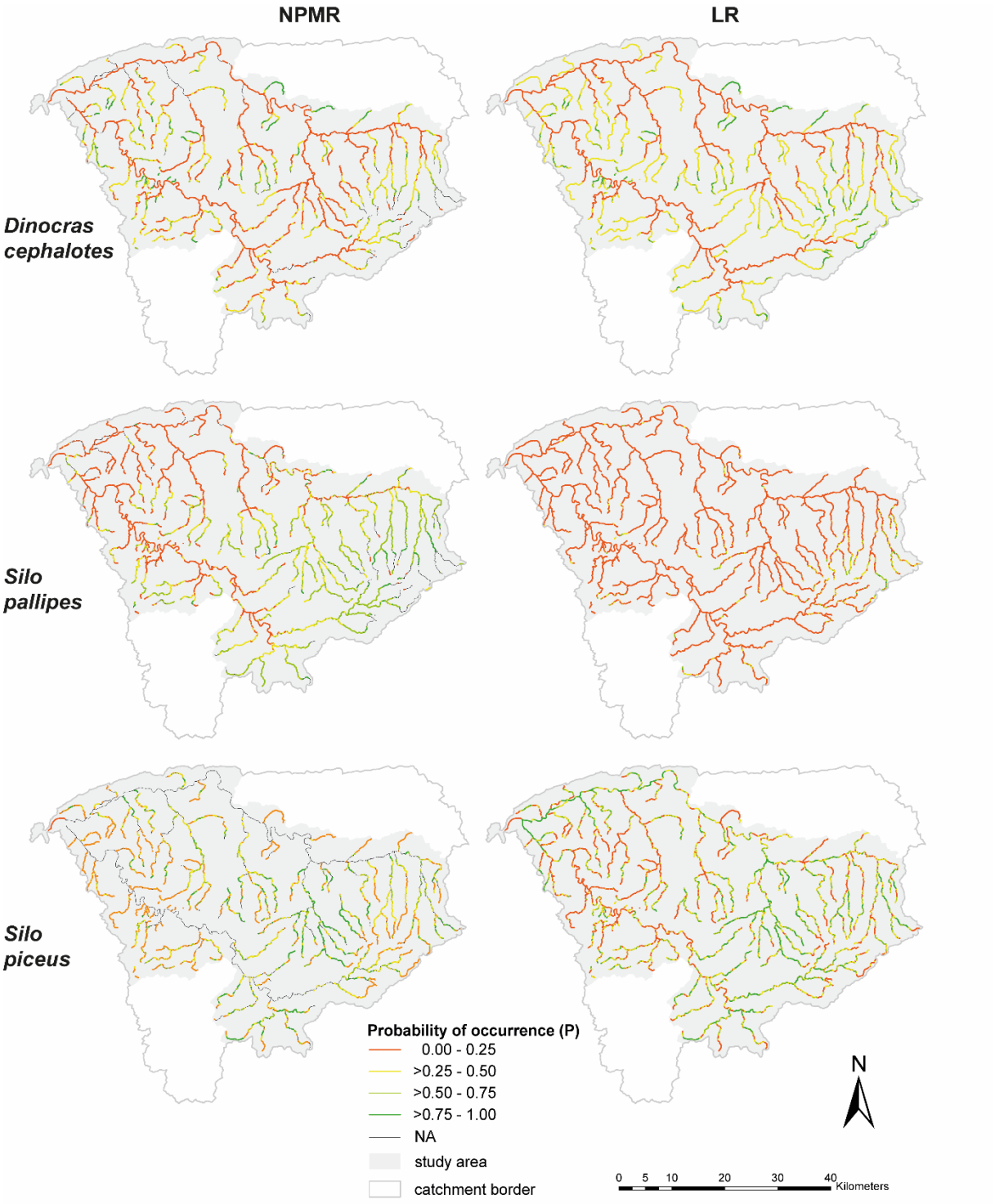

Figure 5.3: Predictive maps of three model species showing the probabilities of occurrence (%) based on non-parametric multiplicative regression (NPMR) and logistic regression (LR) models at a river section scale of 100 m. The threshold for splitting probabilities of occurrences into presence and absence was set to P = 0.5. While LR produced consistent predictions for every river section, NPMR assigns a missing value instead of an estimate of probability if the neighborhood size of this sampling point is smaller than the criterion minimum (set to 25% of the average neighborhood size, black lines). Prediction maps of all model species are provided in Appendix 3b.

Table 5.3: Main results of non-parametric multiplicative regression (NPMR) and logistic regression (LR) models based on the 2010 field data. Significance of the NPMR models was tested by a Chi^2 test with p = probability of type I error from Chi^2 distribution (d.f.=1) with significance level <0.05. Significance of LR-models was tested by a Hosmer-Lemeshow goodness-of-fit statistic (H-L) indicating a poor fit if the significance value is less than 0.05.

	NPMR				LR		
Model species	**logB**	**xR²**	**Chi² p**	**crossAUC**	**Nagelkerke R²**	**H-L p**	**crossAUC**
Gammarus pulex (LINNAEUS, 1758)	7.61	0.27	<0.0001	0.74	0.23	0.313	0.61
Siphlonurus lacustris (EATON, 1870)	3.81	0.24	0.0001	0.82	0.26	0.072	0.79
Calopteryx virgo (LINNAEUS, 1758)	3.34	0.06	0.0190	0.65	0.17	0.912	0.49
Leuctra geniculata (STEPHENS, 1836)	5.70	0.22	<0.0001	0.76	0.21	0.277	0.47
Dinocras cephalotes (CURTIS, 1827)	8.92	0.35	<0.0001	0.84	0.36	0.917	0.80
Perla marginata (PANZER, 1799)	6.12	0.17	0.0900	0.61	0.26	0.673	0.70
Silo pallipes (FABRICIUS, 1781)	9.16	0.34	<0.0001	0.85	0.50	0.039	0.66
Silo piceus (BRAUER, 1857)	11.17	0.45	<0.0001	0.91	0.39	0.022	0.80
Hydropsyche dinarica MARINKOVIC, 1979	7.32	0.30	0.0001	0.78	0.41	0.927	0.75
Hydropsyche incognita PITSCH, 1993	3.26	0.12	0.0020	0.79	0.25	0.014	0.70
Hydropsyche instabilis (CURTIS, 1834)	8.69	0.30	<0.0001	0.72	0.32	0.152	0.73

Table 5.4: Pearson correlations of species prevalence (prev.), model performance measures (xR² / Nagelkerke R²) and predictive performance measures (cross-validated AUC, PCC and TSS, field validated AUC, PCC and TSS) using the 2010 data for model development and the 2011 data for model validation in non-parametric multiplicative regression (NPMR). The significance of correlations was tested using a t-test after checking for distribution normality (Shapiro-Wilk-test) using the following significance levels: p<0.05 = *, p<0.01 = **, p<0.001 = ***

	Prevalence 2010	**xR² / N. R²**	**crossAUC**	**crossPCC**	**crossTSS**	**Prevalence 2011**	**fieldAUC**	**fieldPCC**	**fieldTSS**	**Prevalence survey**	**indAUC**	**indPCC**	**indTSS**
Prevalence 2010	-												
xR²	0.37	-											
crossAUC	-0.21	**0.74****	-										
crossPCC	-0.58*	0.25	**0.63***	-									
crossTSS	0.17	**0.88*****	**0.74****	0.52	-								
Prevalence 2011	**0.66***	-	-	-	-	-							
fieldAUC	0.31	0.55	0.25	-0.14	0.42	0.44	-						
fieldPCC	**-0.77****	-0.30	0.29	0.55	-0.19	-0.57	-0.14	-					
fieldTSS	0.24	0.44	0.28	0.01	0.41	0.36	**0.86*****	0.12	-				
Prevalence survey	0.59	-	-	-	-	-	-	-	-	-			
indAUC	0.33	0.16	-0.06	-0.10	0.00	0.21	0.31	0.07	0.39	0.39	-		
indPCC	**-0.83****	-0.40	0.12	0.55	-0.14	-0.46	-0.07	**0.73***	0.07	-0.58	-0.27	-	
indTSS	**0.62***	0.25	0.01	-0.22	0.04	0.40	0.23	-0.10	0.38	0.59	**0.82****	-0.54	-

Table 5.5: Pearson correlations of species prevalence (prev.), model performance measures (xR² / Nagelkerke R²) and predictive performance measures (cross-validated AUC, PCC and TSS, field validated AUC, PCC and TSS) using the 2010 data for model development and the 2011 data for model validation in logistic regression (LR) models. The significance of correlations was tested using a t-test after checking for distribution normality (Shapiro-Wilk-test) using the following significance levels: p<0.05 = *, p<0.01 = **, p<0.001 = ***

	Prevalence 2010	xR² / N. R²	crossAUC	crossPCC	crossTSS	Prevalence 2011	fieldAUC	fieldPCC	fieldTSS	Prevalence survey	indAUC	indPCC	indTSS
Prevalence 2010	-												
N. R²	0.13	-											
crossAUC	-0.05	0.56	-										
crossPCC	**-0.65***	0.14	**0.60***	-									
crossTSS	0.28	0.39	**0.73***	0.39	-								
Prevalence 2011	**0.68***	-	-	-	-	-							
fieldAUC	0.16	0.35	0.60	0.50	0.36	0.41	-						
fieldPCC	-0.20	-0.08	0.07	0.55	-0.01	-0.16	**0.66***	-					
fieldTSS	0.30	0.02	0.47	0.45	0.58	0.40	**0.81****	**0.66***	-				
Prevalence survey	0.58	-	-	-	-	-	-	-	-	-			
indAUC	0.46	0.38	0.06	-0.17	0.49	0.42	0.17	-0.13	0.23	0.23	-		
indPCC	**-0.75****	0.13	0.29	0.53	-0.29	-0.21	0.18	0.14	-0.18	**-0.66***	-0.38	-	
indTSS	**0.61***	0.28	0.49	0.07	**0.81****	**0.63***	0.43	-0.04	**0.63***	0.01	**0.64***	-0.41	-

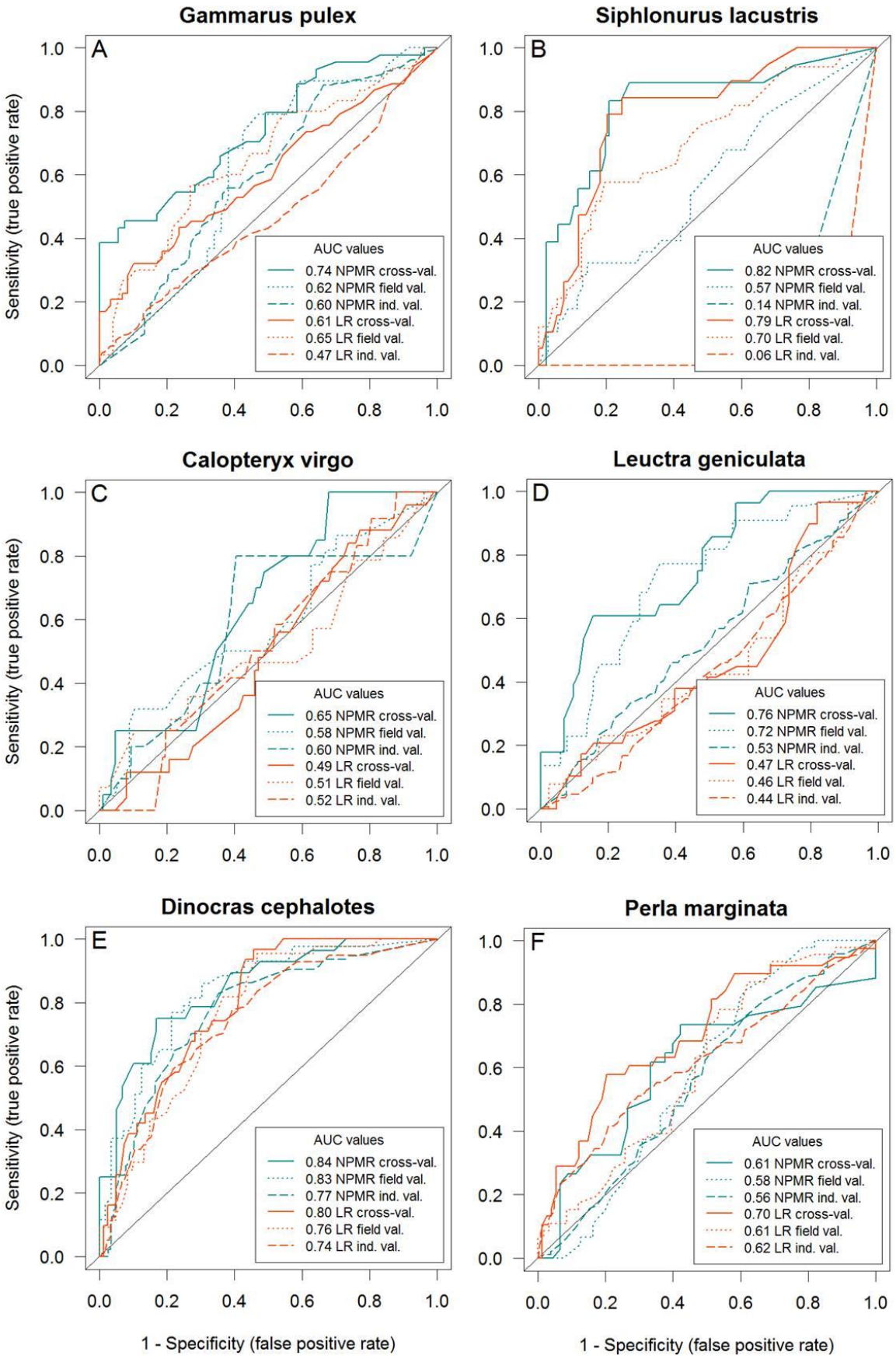

Figure 5.4a: ROC plots comparing cross-validated AUC (solid lines), field-validated AUC (pointed lines) and independent validation (dashed lines) of non-parametric multiplicative regression (NPMR, blue) and logistic regression models (LR, orange).

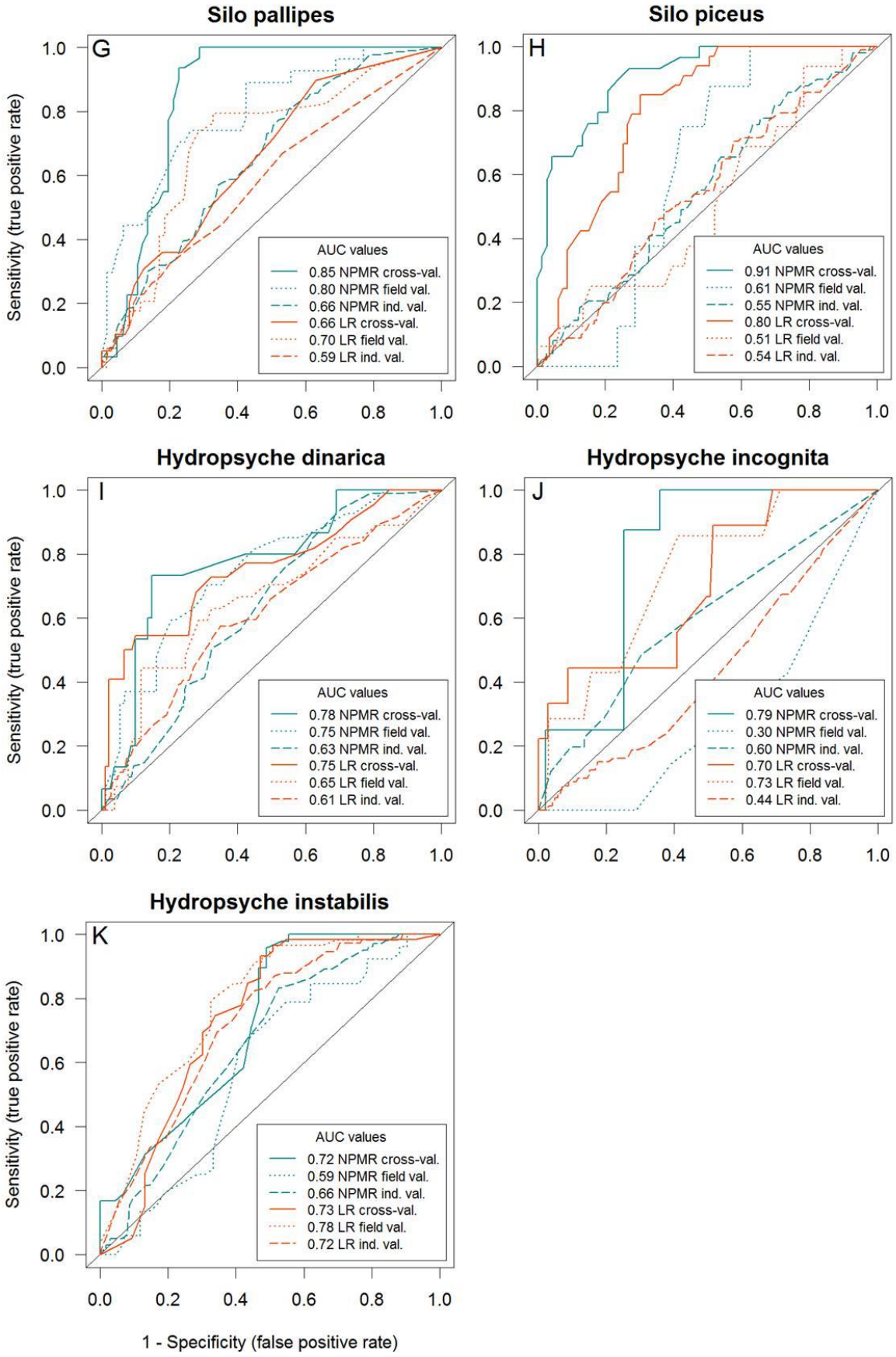

Figure 5.4b: ROC plots comparing cross-validated AUC (solid lines), field-validated AUC (pointed lines) and independent validation (dashed lines) of non-parametric multiplicative regression (NPMR, blue) and logistic regression models (LR, orange), continued.

When related to the species prevalence, the validation statistics revealed consistent patterns. The proportion of true positive predictions (TP%) increased with increasing prevalence (Figure 5.5), thus showing that correctly predicted presences are related to the actual number of presences in the training dataset. Similarly, but with a different sign, the overall percentage of correctly classified instances (PCC; i.e. true presences and true absences together) decreased with increasing prevalence as coherent to the percentage of true negative predictions (TN%). For all validation approaches, a consistent decline of TN% with increasing prevalence was obvious, thus suggesting a strong dependency between TN% and the number of actual presences (or absences) in the underlying dataset. Overall, the predicted true absences ranged from 15–90%, while true presences ranged significantly lower and achieved values between 0 and 40%. Besides this, percentages of true presences increased with prevalence in cross- and field validation approaches at a similar extent while; for independent validation, the slope was much lower. Besides PCC, TP and TN, AUC and TSS were independent of prevalence (Appendix 3d). These relationships were found irrespective of the regression methodology and validation approach.

When comparing the means of all SDM performance measures across the three validation approaches (Figure 5.6), overall, the averaged TP and TSS scores indicated a much lower SDM performance than AUC and PCC. The mean PCC score (between 70 and 80%) increased for the independent validation approach, coherent to the increasing scores of true negatives (TN). TN and thus PCC showed an increase from field to independent validation while the means of AUC, TSS and TP continuously decreased from cross-validation to field and independent validation.

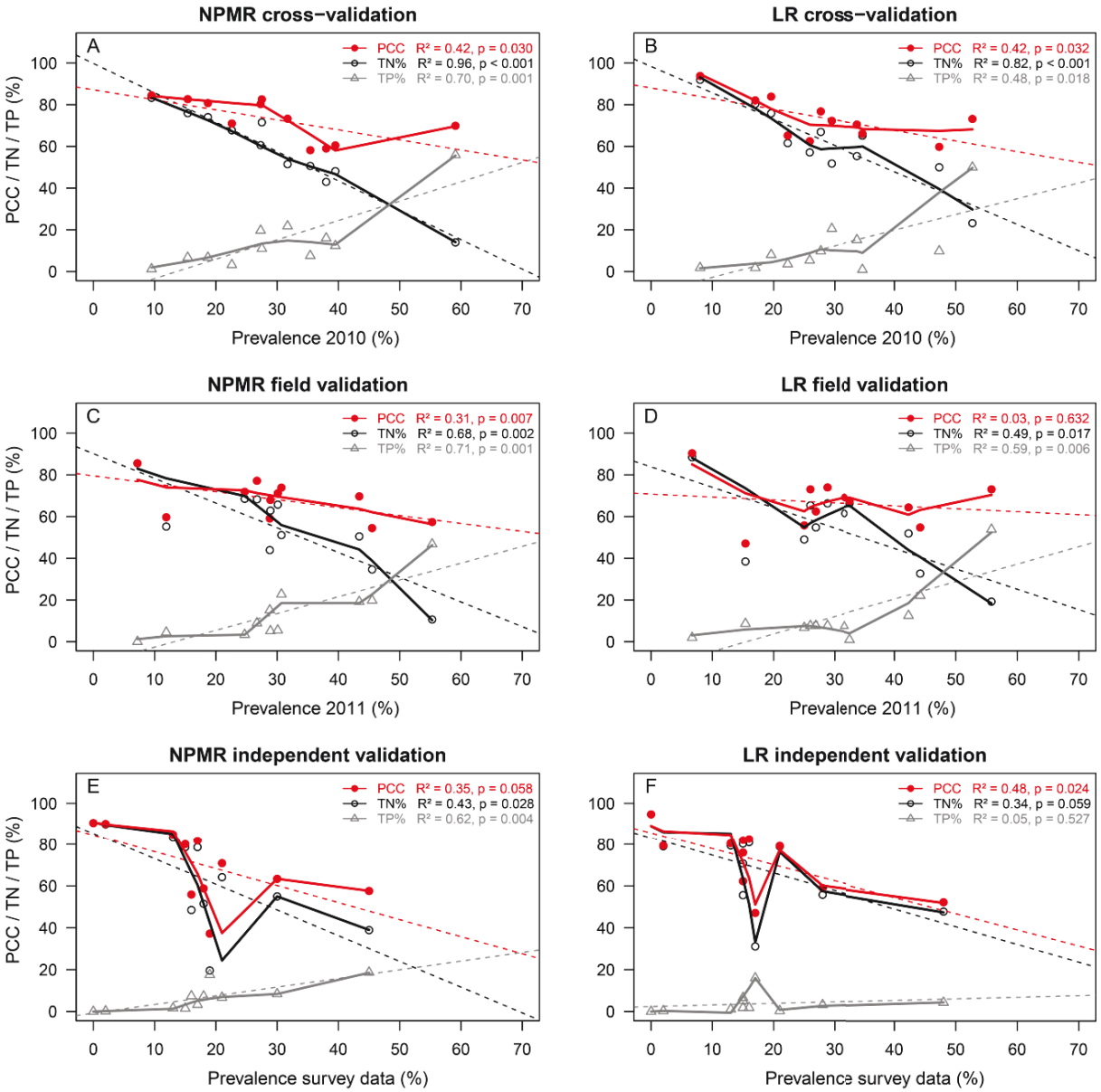

Figure 5.5: Comparison of model prediction performance measures (percent correctly classified [PCC], true negative predictions [TN%] and true positive predictions [TP%]) against species prevalence. All models (non-parametric multiplicative regression (NPMR) and logistic regression models (LR)) were developed using data from 2010, whereas data from 2010 were used for cross validation (A + B) and data from 2011 for field validation (C + D). Presences and absences were split at a threshold of 0.5. Adjusted R^2 values were derived from linear regressions (dashed lines, significance based on the model's F statistics). Solid lines were generated using a lowess smoothing function.

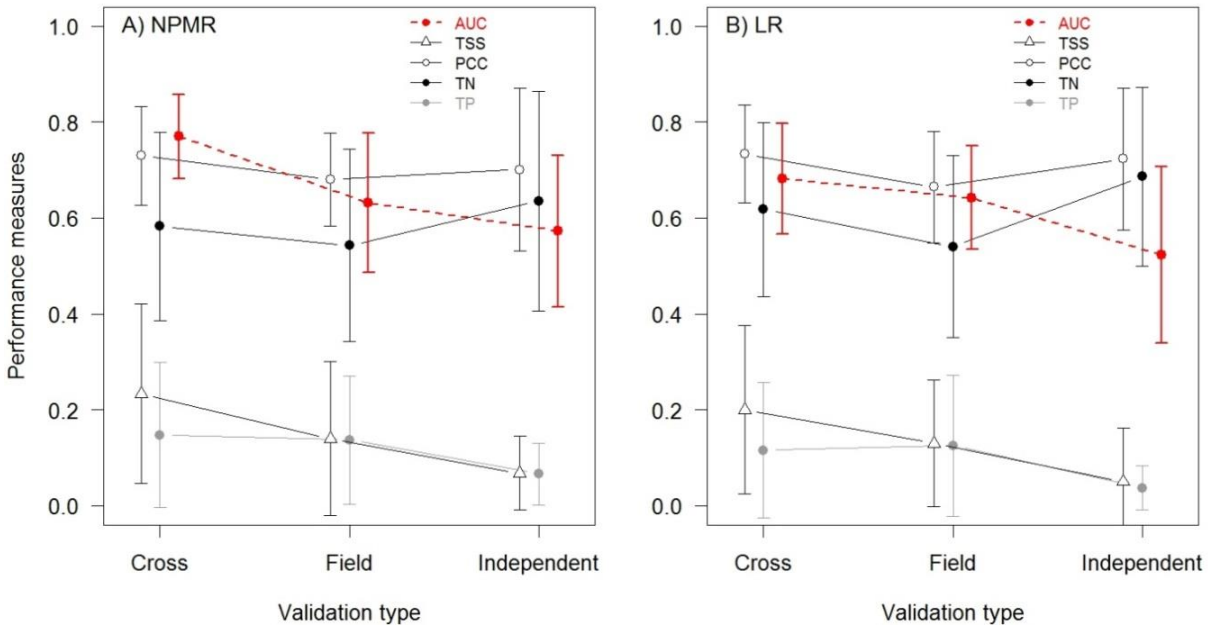

Figure 5.6: Comparison of the means of the performance measures (AUC, TSS, PCC, TN and TP) across all three validation approaches. Means are calculated for all eleven species, separated by the SDM method. The standard deviation is given by vertical whiskers.

5.4 Discussion

5.4.1 Model and predictive performance

In this study, macroinvertebrate SDMs were based on 32 proxy descriptor variables which may explain their overall moderate to weak SDM performance. Beside broad-scale factors aquatic macroinvertebrate larval habitats are also formed at comparatively fine scales, i.e. at the scale of several up to hundreds of square meters. Obviously, important fine-scale habitat variables remained unaddressed with this variable selection. Hence, although the surrogate environmental variables can be linked to more direct habitat conditions, land use and physical habitat quality at broader (reach to sub-catchment) scales turned out to be poor predictors of species distributions in the study area (see also Bahn & McGill 2013). This points at a dilemma in data availability. Broad-scale proxies are available at regional or even larger extents, while fine-scale microhabitat variables required for SDM are usually recorded at the scale of square meters to hundreds of square meters in streams or rivers. It is unlikely that such fine-scale data can be compiled at the scale of entire watersheds, which would be a prerequisite to predict the occurrence of species at that scale. A more promising approach might be to further highlight the ultimate habitat requirements of the species and then test further broad-scale variables for their relationship with habitat requirements.

In addition, water quality variables might constitute suited proxies for species occurrence. Previous modelling revealed a significant contribution of nitrate or electric conductivity to

several models. These variables were omitted later from the set of predictors, because they represented only single (non-representative) spot measures and were available only for <2.1% of 100 m sections in the entire model catchment. Hence, a better understanding of the linkages between broad-scale environmental proxies and fine-scale habitat variables is inevitable to improve SDMs. For example, water quality and biological variables might have significantly contributed to the goodness-of-fit of the SDMs and deserve better consideration in future studies (e.g. Araújo & Luoto 2007, Bizzi et al. 2012, Lock & Goethals 2013, Le Roux et al. 2013, De Araújo et al. 2014).

Uncertainty in SDMs (weak species-environmental relationships) can also arise from data deficiencies (Barry & Elith 2006), i.e. errors in species' predicted distributions including false negatives and false positives. Commission errors arise from predicting a species where it does not occur, i.e. the percentage of false positive predictions (FP). The commission error incorporates three assumptions that may cause false positive predictions: the focal species may i) be present but undetected due to a sampling error, or ii) it is truly absent due to dispersal limitations, historical factors, local extinctions or biotic interactions despite of environmentally favorable conditions (presence outside the realized but inside the fundamental niche, apparent commission) or iii) it is truly absent due to environmental factors not considered in the SDM (see above) or taking into account environmental factors that do not fit the actual species' niche (presence predicted outside both the realized and fundamental niche, real commission) (Peterson 2001, Guisan & Thuiller 2005). Across both validation approaches and modelling methodologies, prediction of absences was more often successful (high TN rate) but also failed more frequently (high FN rate) than prediction of presences, although a very detailed sampling campaign was carried out reducing the error of leaving present species undetected. The commission error (false positive rate) was mostly lower than the omission error (false negative rate) across all SDMs (see Appendix 3e).

Despite modest species-environment correlations in the SDMs, some models yielded high predictive power out of ROC cross-validation with AUC values exceeding 0.80 but in turn, high predictive performance did not necessarily correspond to high model fits. Thus, conclusions about how well a model discriminates predictive probabilities into presence and absence (predictive performance) cannot be drawn from a model's goodness-of-fit alone, as the correlations between both performance measures were very tenuous indicating decoupled information of xR^2 and AUC. Actually, AUC ignores the goodness-of-fit of the models (Lobo et al. 2008). Contrastingly, if used as the single performance criterion, AUC neglects important SDM properties like costs of commission and omission errors (Lobo et al. 2008, Jiménez-Valverde 2012). Others reported the value of TSS statistics (e.g. Eskildsen et al. 2013), but the high correlation of TSS and AUC in this study questions the added value of reporting TSS. Furthermore, models expressing the same or similar AUC values may predict very different

patterns of distributions (Austin 2007), costs of commission and omission errors (Lobo et al. 2008, Jiménez-Valverde 2012) and thus, correctly predicted presences and absences. Thus, it should not be reported as a single measure of a model's performance. Reporting both measures of model performance and predictive performance is therefore recommended.

5.4.2 Comparison of cross-, field and independent validation

Field validation as applied in this study is not very common in studies on ecological modelling due to its resource and time consuming effort. This validation approach achieves a dependent validation data set which directly tests the model's predictions in the field giving a more realistic comparison of predictions to actual species occurrences than cross-validation alone. By applying this validation approach, sampling errors (e.g. due to different sampling methods) have been largely avoided in this study. Prediction errors such as false positives (FP) and false negatives (FN) could be reduced by a) applying sampling methods that consider the targeted species habitat preferences and b) by performing a second sampling campaign for validation that directly examines SDM predictions. Detected absences were assumed to be true absences in both campaigns, because each site was intensively sampled for 45 minutes. As there are no significant differences in false positive rates between all validation approaches, I draw the conclusion that commission type ii) and type iii) (as mentioned before) are the main drivers for this finding. Distinction between the three types of commission is hardly possible and, therefore, dispersal limitation, legacy effects and undetected environmental determinants for species occurrence (especially fine-scale variables) can just be assumed to be the main causes of commission error.

The comparison of performance measures out of cross-, field and independent validation showed that in most cases cross-validated AUC revealed values higher or equal to field and independent validated AUC. This demonstrates that the internal comparison of observations used for model training and validation (i.e. cross-validation) tends to over-estimate the discriminatory power of SDMs (Brotons et al. 2004, Araújo et al. 2005, Bahn & McGill 2013). In contrast, independent validation based on a high number of survey data revealed much lower predictive performances. This is most likely caused by differing sampling procedures used to monitor macroinvertebrate assemblages. As the target of monitoring macroinvertebrate communities is to assess the riverine ecological status, the standard multi-habitat sampling method is used which might ignore specific and rare habitats at a certain rate. Moreover, the taxonomic identification is performed at a taxa level rather than up to the species level. Hence, field validated performances took an intermediate position between cross- and independent validation suggesting that field validation is more conservative and probably also more appropriate to validate the predictive accuracy of an SDM. This finding agrees with

several former studies showing overly optimistic assessments of predictive performance via cross-validation when compared to independent validation or data splitting (Brotons et al. 2004, Araújo et al. 2005, Bahn & McGill 2013,). This study highlights the importance of testing properly the predictive performance of SDMs by comparing observations and predictions as well as by using different validation approaches based on new field data in place of cross-validation and independent validation.

The overoptimistic prediction success of cross-validated models may be caused by i) using the same data for model training and validation (named as 'resubstituition' by Araújo et al. 2005), ii) by temporary unstable species occurrences due to seasonal changes, dispersal, local disturbances, biotic interactions and niche ecology and iii) by extrapolating modelled species-environment relationships into new climatic and biotic space that may include extrapolation to non-analog environmental conditions not encountered at the training locations (Bahn & McGill 2013). However, SDMs represent a static state whereas natural variability is commonly not considered in the assessment of predictive performance. In fact, dynamic processes are of substantial importance for freshwater species. Moreover, environmental conditions may be consistent within the region of interest, but may vary locally (non-stationarity, Miller 2012). As an example for riverine systems, macroinvertebrate communities characteristically change along the river course due to varying flow conditions and corresponding changing habitat conditions (coarse stony substrates in the upper stream sections to gravel and sandy substrates in the lower stream sections), but local geomorphological and biogeographical conditions may interrupt this continuum leading to different biotic communities than expected. This can hardly be avoided as separate regions with the same species complement, ranges and combinations of environmental predictors and ecological history simply do not occur (Araújo et al. 2005). I conclude that field validation is more conservative and probably more appropriate to validate the predictive performance of SDMs than using cross-validation or survey data.

5.4.3 Dependency on species prevalence

Probabilistic occurrences as a result of SDMs are described to be highly dependent on the relative proportion of presences in the sample and thus, predictive performance metrics are biased towards the highest number of either presences or absences (Jiménez-Valverde & Lobo 2006). The apparently negative effect of prevalence on the performance of SDM predictions has frequently been judged to be of major importance when validation is performed (e.g. McPherson et al. 2004, Jiménez-Valverde & Lobo 2006, Jiménez-Valverde et al. 2009). In this study, overall threshold-independent measures on model performance (xR^2) and predictive performance (AUC, TSS) were not correlated to the initial prevalence (Appendix 3d).

The AUC statistic previously has been described as independent on prevalence (Manel et al. 2001, McPherson et al. 2004, Allouche et al. 2006). However, I also showed high AUC values for rare species (*Silo piceus*, *Hydropsyche incognita*) obtaining high amounts of absences both in the training and validation data. A critical assessment of the effects of prevalence on the overall predictive accuracy is problematic because prevalence is likely to vary with both species ecological characteristics and relative sampling effort (Brotons et al. 2004). Former studies found SDM predictions to be usually more accurate (corresponding to high AUC scores) for species with smaller range sizes, a higher habitat specificity and high rarity than for common species most of which are also generalists (Brotons et al. 2004, Segurado & Araújo 2004, Elith et al. 2006, McPherson & Jetz 2007, Tsoar et al. 2007, Lobo et al. 2008, Jiménez-Valverde et al. 2008, Franklin et al. 2009). Less tolerant species with specific environmental requirements tend to be less frequent (Brown et al. 1995). Additionally, lower sampling effort or bias in the data collection may also decrease species prevalence. Prevalence is thus likely to affect predictive performance more strongly via indirect effects of species' ecology (Brotons et al. 2004).

Contrary to AUC, threshold-dependent measures are highly affected by prevalence in the training and test data set (Fielding & Bell 1997, Manel et al. 2001, Guisan & Thuiller 2005). PCC, true positive and negative rates and false positives and negative rates showed a strong relationship with prevalence among different methodologies and validation approaches. Low prevalences yield high true negative rates (TN%) and low true positive rates (TP%). Higher prevalences yield lower TN% and higher TP% rates. This finding, which was obvious in all validation approaches, coincides with the theoretical analyses of performance criteria by Mouton et al. (2010) indicating higher PCC values when prevalence declines. Therefore, due to a statistical artefact, high proportions of correct prediction may arise especially for extremely rare species that are usually in the focus of ecological modelling studies. When prevalence declines, absences are much more likely to be effectively predicted than presences (Fielding & Bell 1997, Manel et al. 2001). In this study, the slope of the true positive rate – prevalence relationship was much lower but positive compared to the true negative rates. Contrary to PCC, TP and TN, the TSS had no correlation with prevalence. This finding is congruent to Allouche et al. (2006) indicating that high rates of correctly predicted presences cannot be reached at low prevalence levels.

Moreover, for common species, rates of correctly predicted presences exceed those of correctly predicted absences by showing probably an exponential behavior towards higher prevalences (80–100%). However, the observed prevalence in this study did not exceed 60% within training and validation data. High macroinvertebrate prevalences at a species level are practically unfeasible for most species and interpretation of PCC patterns at prevalences >60% is beyond this study. Manel et al. (2001) found the overall prediction success (PCC) of

macroinvertebrate (Ephemeroptera, Plecoptera, Trichoptera) SDMs to vary curvi-linearly and highly systematically with prevalence. Following this, I expect the prediction success (PCC) to grow when prevalence reaches a high level (70–100%). This reflects the composite effects of sensitivity (increasing with increasing prevalence) and specificity (decreasing with increasing prevalence). However, when prevalence is medium, PCC is slightly lower indicating arising proportions of error (FP and FN). Particularly in such cases, testing predictive performance only based on overall accuracy metrics such as AUC may be misleading in what and how a model is predicting in detail. Single performance measures out of a confusion matrix (such as TN and TP) may yield additional valuable information on prediction errors (Vaughan & Ormerod 2005).

5.4.4 Selecting thresholds

As conventional threshold a value of 0.5 has already been used in ecology (Manel et al. 1999b; 2001, Luck 2002, Stockwell & Peterson 2002, Bailey et al. 2002, Woolf et al. 2002). As the intention of this study was to compare the effects on different validation approaches and species prevalence on the SDM predictive performance, a threshold of 0.5 was selected for the computation of predictive performance measures. However, this choice has been critized to be very arbitrary and lack any ecological basis (Osborne et al. 2001). Many other statistical methods derived from confusion matrices are existent to gain information on best threshold values. The ROC procedure offers a way of identifying an optimum probability threshold which splits the range of probability into binary information on predicted species' occurrences. A common threshold is the maximum value of the Cohen's kappa statistic (Cohen 1960) which has been widely used in conservation biology (Randin et al. 2006, Freeman & Moisen 2008, Jiménez-Valverde 2012) but was critized for its strong dependence on species prevalence (Allouche et al. 2006). Zweig & Campbell (1993) as well as Manel et al (2001) stated an easy way of threshold definition by simply reading the point on the ROC curve at which the sum of sensitivity and specificity is maximized. This is equivalent to finding a point on the ROC (receiver operating characteristics) curve (i.e. sensitivity against 1-specificity) whose tangent slope is equal to 1 (Cantor et al. 1999). The point at which sensitivity and specificity are equal can also be chosen to determine the threshold (Cantor et al. 1999). Another approach is to select the point on the ROC curve that has the closest distance to the upper-left corner in the ROC plot since the point in this corner represents a perfect classification with 100% sensitivity and specificity (Cantor et al. 1999). Liu et al. (2005) recommended that a good presence/absence prediction would be obtained by taking the prevalence of model-building data as the threshold.

However, there is no uniform perspective existing and selecting an optimum threshold for use of threshold-dependent performance measures depends on the costs of different types of misclassification (commission and omission error) (Liu et al. 2005). An additional obstacle is the fact that the effect of the threshold on misclassification errors depends on the prevalence (Franklin 2009). For instance, Freeman & Moisen (2008) found that, for species with high predictive performance (AUC) and prevalence near 50%, the optimal thresholds tend to converge. With low prevalence, different criteria can result in quite different thresholds. Liu et al. (2005) stated that using a set of different approaches to select the optimal threshold (observed prevalence, average predicted probability, the sum of sensitivity and specificity, sensitivity equal specificity, the point on the ROC plot nearest the upper left corner) all gave roughly the same results. However, the selection of an optimal threshold intensively depends on the intended use of the model (Franklin 2009). In my purpose, different validation data and performance criteria were tested and the effect of species prevalence was described so that the conventional threshold of 0.5 was chosen to keep comparability.

6 Summary, conclusions and future prospects

6.1 Background

This thesis investigated the usefulness of broad-scale variables as predictors on modelling distributions of single macroinvertebrate species, the spatial transferability of the distribution models and the application of field validation. Species distribution models (SDMs) allow the prediction of the spatially explicit presence and absence of species based on environmental predictors that reflect the species' habitat requirements. Thus, SDMs constitute a useful tool to predict the distribution of occurrences or abundances across a landscape, sometimes requiring extrapolation in space and time (Elith & Leathwick 2009). SDMs therefore provide an appropriate way to gain information on species occurrences within one catchment without need to produce a catchment-wide sampling data. Hence, the use of SDMs is a cost- and time-effective alternative. SDMs for riverine systems rise specific demands, as they are heterogeneous, directional highly structured networks, connected laterally, longitudinally and vertically (Ward 1989, Linke et al. 2008). According to the Water Framework Directive (WFD, European Commission 2000) degraded rivers should be restored to achieve good 'ecological status' until 2015 assessed by characterizing assemblages of fish, benthic invertebrates and aquatic flora (Hering et al. 2010). In this regard, SDMs may provide useful tools to determine the actual distribution, to predict potential donor populations for the recolonization of a restored section or to compute potential changes in the ecological status due to restorations. Macroinvertebrate communities strongly respond to present conditions at the local scale (water quality, substrate availability) as well as the broad catchment scale (e.g. upstream land use and hydromorphological conditions). Especially local variables are mostly monitored at single river sections but for the construction of SDMs and their application as prediction tool, continuous variables along entire river networks are obligatory. This fact points at a dilemma in the data availability. In this study, broad-scale variables as surrogate predictors of macroinvertebrate distribution were used to train and validate SDMs in a mountainous river catchment. The presence/absence of macroinvertebrate species was extensively scanned by two field campaigns in two years (2010 and 2011). The entire data set of 225 sampling sites was split up spatially (Lenne watershed and upper Ruhr watershed) to develop SDMs based on broad-scale predictors and to gain first insights into the transferability of SDMs between adjacent watersheds. In a next step, the data set was split up temporally (2010 and 2011) to

properly validate the models using field data of equal sampling design and compare the results to internal cross-validation and independent survey data.

The aims and related hypotheses (H) of this thesis were:

1. the detailed description of the species' actual distribution and the determination of their ecological requirements including a literature cross-check (chapter 3)

2. testing the applicability of distribution models based on broad-scale predictors and the comparison to models using fine-scale predictors (chapter 4)
   H2a: SDMs based on broad-scale predictors as proxies for local conditions achieve acceptable performance.

   H2b: The inclusion of local, fine-scale predictors like physico-chemical variables and substrates lead to a significant improvement of SDM performance.

3. testing the transferability of the model's spatial predictions to adjacent regions (chapter 4)
   H3: SDM predictions for adjacent watersheds based on the same environmental data are spatially transferable due to the similar environmental characteristics of both watersheds.

4. properly validating distribution models using different data sets for validation (chapter 5)
   H4: Validating SDM predictions by a new field campaign (field validation) obtains a more realistic assessment of SDM predictive performance than internal cross-validation or using independent survey data alone.

5. determining the effect of species prevalence on the model's performance (chapters 5)
   H5: SDMs of less prevalent species tend to over-predict species absences rather than presences.

The third chapter focused on the description of the species' actual distribution, the determination of their substrates preferences and ecological requirements according to riparian land use classes, physical habitat quality classes and physico-chemical variables that were measured on-site at each of the 225 sampling sites. The fourth chapter investigated the applicability and transferability of SDMs for macroinvertebrates using broad-scale predictors (land use, physical habitat quality). The broad-scale models were compared to models using additional local variables (substrates, physico-chemistry). The SDMs were built separately for the Lenne and upper Ruhr watersheds and then, model predictions were transferred to the adjacent watershed, respectively. The fifth chapter focused on the validation of macroinvertebrate SDMs using different data sets (cross-validation, field validation,

independent validation) and different performance measures. The effect of species prevalence was discussed in both, the fourth and fifth chapter.

In the following sub-chapters, the methods, results and main findings of each study with regard to the aims specified above are presented.

6.2 Species profiles

Macroinvertebrate species are a widespread, abundant and highly diverse group of aquatic organisms that inhabit all types of water bodies. In freshwater bodies, macroinvertebrates form a basis for the river assessment in Europe due to their strong response to water quality but also hydromorphological degradation and catchment characteristics. Thus, macroinvertebrates are commonly applied indicators of ecosystem health. In this thesis, eleven macroinvertebrate species were selected which covered several life cycles, feeding types and specific preferences of habitats. Overall, no strong correlations between species occurrences and land use, physical habitat quality, substrates and physico-chemistry were obvious. However, in particular, some environmental variables showed significant relationships to the species presence/absence. These ecological preferences were properly described based on land use data (ATKIS 2007), physical habitat quality, substrates and physico-chemistry and cross-checked with relevant literature.

Hydropsyche instabilis was most frequently found in the study area (52%), while *Hydropsyche incognita* was the rarest with a prevalence of 8%. Mapping the presence/absence of the species showed species-specific distribution patterns in this region. In general, a lack of distribution of nearly all species was found in the southern tributaries of the Lenne (upstream to the Bigge confluence) which may be caused by former pollution, acidification and degraded hydromorphology. In contrast, the watersheds very near to the Lenne source show a strong increase in species numbers compared to the river sections downstream. This finding points at the recolonization via the upper Ruhr tributaries that directly adjoin to the Lenne watersheds.

Aim 1 *the detailed description of the species' actual distribution and the determination of their ecological requirements including a literature cross-check* was accomplished.

Concluding remarks:

Environmental data were available for each sampling site covering different broad-scale and fine-scale (local) variables that were thoroughly collected during two sampling campaigns. The

species' ecological requirements were adequately described based on significant species-environment-relationships. Thus, a high-quality data set on environmental conditions and species presence/absence was available for further analysis. The species profiles within the study area contribute to the knowledge of the actual distribution patterns and possible population expansions.

6.3 SDMs based on broad-scale predictors and transferability

The habitats of macroinvertebrates are often defined at very fine scales spanning one to several tens of square meters (e.g. substrate preferences). Such habitat information, however, is usually not available for entire river networks at the large scale, which limits the application of SDMs in conservation ecology. In this study, I presented SDMs of eleven lotic macroinvertebrate species based on two broad-scale environmental variable groups: land use (derived from ATKIS high resolution land cover map) and physical habitat structure (derived from regional surveys in Germany). The actual species distributions were scanned through a field survey at 225 sites in two adjacent watersheds in a mountainous region (the rivers Ruhr and Lenne, Federal State of North Rhine-Westphalia, Germany). The SDMs were built using a non-parametric multiplicative regression method (NPMR). The aim of this study was, first, to test the usefulness of broad-scale variables in SDMs using measures of model goodness-of-fit and predictive power. Second, local habitat variables (physico-chemistry and meso-scale substrates) were included in SDMs to examine model improvement. Third, the transferability of models of the same species between the two watersheds was tested. Due to the similar environmental characteristics of both watersheds, I hypothesized concordant SDMs for both watersheds.

Overall, reliable performance and predictive power were found for models of *Dinocras cephalotes* in both watersheds. Models of several other species performed fair in the river Ruhr (*Leuctra geniculata, Silo piceus, Siphlonurus lacustris*) but not in the Lenne system or vice versa (*Hydropsyche instabilis*). Broad-scale SDMs included predictors on physical habitat quality as well as riparian land use at a similar extent. For five out of eleven species, the SDMs including fine-scale predictors (e.g. physico-chemistry, microhabitat distribution) outperformed those models using broad-scale predictors only (AUC > 0.70). I suggest that species specifically distributed in upstream reaches explicitly respond to fine-scale variables due to stronger dependency of their occurrences on local conditions. SDMs of *Hydropsyche incognita* showed very high predictive performances in both watersheds despite of having weak model accuracy. This indicates the relative impact species prevalence on predictive performance when the focal species is rarely present. Model transferability from one watershed to another was low (transferability index < 0.60), thus revealing SDMs not only to be species-specific but

also variable across adjacent watersheds. I suggest that the transferability is limited not only by actual environmental differences between both watersheds, but also by legacy land use effects that may continue to affect the recent distribution of macroinvertebrates.

This study focused at aim 2 and 3:

2. testing the applicability of distribution models based on broad-scale predictors and the comparison to models using fine-scale predictors (chapter 4)

   H2a: SDMs based on broad-scale predictors as proxies for local conditions achieve acceptable performance.

   - The hypothesis was partly confirmed by the results. SDM performances differed species-specific.

   H2b: The inclusion of local, fine-scale predictors like physico-chemical variables and substrates lead to a significant improvement of SDM performance.

   - The hypothesis was partly confirmed by the results. Some SDMs showed a considerable improvement by including fine-scale variables but overall, SDM performance was not significantly improved.

3. testing the transferability of the model's spatial predictions to adjacent regions (chapter 4)

   H3: SDM predictions for adjacent watersheds based on the same environmental data are spatially transferable due to the similar environmental characteristics of both watersheds.

   - The hypothesis is rejected.

<u>Concluding remarks:</u>

SDMs based on land use and physical habitat quality at relatively broad-scales led to moderate to weak species-environment relationships in this study. The inclusion of local, fine-scale variables like substrates and physico-chemistry as predictors did not lead to a major improvement of model performances. This implies that major factors controlling riverine species distribution remained undetected.

In general, this study confirms the lack of generality of species distribution, resulting in poor transferability of models between adjacent areas. The results support the need for ecologists and conservation managers to be careful about transferring predictions derived from one

region to another, without knowing the environmental gradients within and between regions as well as individual species conditions. Further research on transferability of predicted macroinvertebrate distributions is required according to river assessment and restoration efforts.

Although the results fail to produce reliable and transferable distribution models which could pass into conservational application, this study provides valuable insights into the complexity and limitations of using broad-scale (proxy) variables at a regional scale.

6.4 Validation of SDMs

Model quality can be expressed as measure of goodness-of-fit (e.g. coefficient of determination), which is straightforward but does not sufficiently address prediction accuracy. Model validation accounting for the correctness of predicted presences and absences of taxa is an additional measure to better judge on a SDM's predictive performance. In this study, the goodness-of-fit and the predictive performance of SDMs on eleven lotic macroinvertebrate taxa were compared, with emphasis on species prevalence in the training data. Two regression methods were applied: non-parametric multiplicative regression (NPMR) and logistic regression (LR). SDMs were based on broad-scale environmental predictors (e.g. land cover, instream habitat quality). The model training was based on the field campaign 2010 (121 sampling sites). The model validation was based i) on the initial training data (leave-one-out cross-validation), ii) on the field data of 2011 whose selection was based on previous model predictions (field validation, 104 sampling sites) and iii) on truly independent survey data (independent validation, 620 sampling sites). Model performance (goodness-of-fit) was calculated as pseudo-R^2 values and predictive performance was expressed as the area under the curve (AUC) resultant from a receiver operating characteristic (ROC) as well as threshold-dependent performance measures (PCC, TSS and true negative and true positive rates).

Overall, SDMs showed acceptable performance measures for the stonefly *Dinocras cephalotes* and the caddisflies *Silo piceus* and *Silo pallipes*. The model's performances were neither positively nor linearly correlated with predictive accuracy (cross-, field and independent validation). The comparison of the three different validation approaches revealed an over-estimation of the discriminatory power of cross-validated models over field and independently validated models. SDM predictive performance (expressed by AUC and TSS) consistently decreased from cross- to field to independent validation. This highlights the intermediate position of field validation between overly optimistic cross-validation and underestimating independent validation. In addition, species prevalence (ranging 8–50%) affected the model's predictive performance: SDMs of less prevalent species tend to over-predict species absences rather than presences. These findings show that the SDM's measure of goodness-of-fit is

decoupled from a model's predictive performance (e.g. AUC). The comparison of validation approaches suggests the use of new field data (instead of training data or survey data based on differing sampling methods), which provide a more reliable basis for SDM quality assessment and a benchmark for comparisons with other methods, such as cross-validation.

This study focused at aim 4 and 5:

2. properly validating distribution models using different data sets for validation

   H4: Checking SDM predictions by a new field campaign (field validation) obtains a more realistic assessment of SDM predictive performance than internal cross-validation or using independent survey data alone.

   * The hypothesis was supported by the results.

4. determining the effect of species prevalence on the model's performance

   H5: SDMs of less prevalent species tend to over-predict species absences rather than presences.

   * The hypothesis was supported by the results.

Concluding remarks:

Concordant to the previous study, SDMs based on broad-scale land use and physical habitat quality assessment lead to moderate species-environment relationships, thus implying the usage of inaccurate factors that do not control riverine species distribution. Yet, the species-environment relationship, expressed as model performance, is not sufficient to assess a SDM's ability to correctly predict the occurrence of a species. The model performance was found to be partly isolated from its predictive accuracy (e.g. percent correctly classified, AUC). Hence, if the focus of research is on the extrapolation of species-environment relationships into space or time, the predictive success of SDMs should be reliably evaluated taking into account both measures of general model fit and predictive accuracy.

The study supports other authors that raise caution against possible bias in (over-)estimates of model-prediction due to a cross-validation approach because the models are optimized to deal with the 'noise' in the data and might consequently lose generality outside the original data (for discussion, see Araújo et al. 2005, Olden & Jackson 2000, 2002). Field validation constitutes an alternative to avoid splitting of small data sets or using independent survey data that may have been collected under different research targets. There is a clear need for studies comparing different validation approaches to classify the practicability of field validation.

Furthermore, low prevalence needs to be considered in defining SDM quality as species rarity is usually a property of data from specialist and/or endangered species that are typically in focus of ecology and conservation management. Freshwater species, especially riverine species, inhabit a very dynamic system expressing very complex life cycles and patchy distribution. This may lead to zero-inflation and an underestimation of prevalence according to the sampling season, sampling method and effort. Thus, assessing predictive performance of SDMs of rare freshwater species poses problems in presence-absence modelling which developers and users of SDMs should bear in mind.

6.5 Future prospects

The application of SDMs on stream macroinvertebrates has developed during the last few years but the usage of surrogate broad-scale predictors at the regional scale is rather new. Thus, it needs to be further developed concerning the accuracy of environmental predictors, especially in terms of potential proxy variables replacing local environmental conditions that are usually not continuously available. The models developed in this thesis were of moderate to poor performance pointing at the lack of environmental variables that correctly describe the species' niche. Moreover, the SDMs performances strongly varied between different species. For instance, the SDM of *Dinocras cephalotes* performed acceptable while SDMs of *Calopteryx virgo* whose habitat requirements are intensively investigated, revealed random results. Obviously, important habitat variables remained unaddressed with the broad-scale variable selection. Hence, although the surrogate environmental variables can be linked to more direct habitat conditions, land use and physical habitat quality at broader (reach to sub-catchment) scales turned out to be poor descriptors of species distributions in the study area. However, the consideration of fine-scale variables did not lead to a highly improved SDM performance. These aspects may point at the need to explore the autecology of macroinvertebrate species, their distribution, dispersal activities and factors affecting their population establishment more intensively. Life cycles of macroinvertebrate species, especially merolimnic species, involve very different stages, from finding suitable locations for hatching to several larval stages, emergence and swarming. At each stage, various abiotic and biotic factors might cause different behavior. The future challenge will be to detect potential bottlenecks of the species' life cycles. A research group has already been proposed to the German Research Foundation (DFG) to address intrinsic (e.g. morphological, physiological and genetic) and extrinsic (e.g. habitat conditions, barriers or parasite load) drivers that affect colonization as a key ecological process, focusing on colonization patterns of individuals, species as well as taxonomic groups.

Since the start of this thesis, integrative modelling approaches were shown to be promising tools in accurately improving modelling performances (Kuemmerlen et al. 2012, 2014) to address relevant hydrologic variables affecting macroinvertebrate species. In addition, integrating relevant dynamic biotic factors like migration of species to newly suitable habitats (Franklin 2010), dispersal capacities, barriers and distances between populations (Sondermann et al. 2015) or dominant species within the community (le Roux et al. 2014) would provide useful extensions of macroinvertebrate predictions. Dispersal is an important driver of dispersion, recolonization and community structure. Linking SDMs to process-based models of species dynamics (species migration and dispersal), population dynamics and landscape dynamics has already been demonstrated to be feasible and informative (Franklin 2010). The combination of hydrodynamic models, substrate and climate models with distribution models as a multi-cascade (e.g. Fukuda et al. 2014) could be a promising but resource-consuming opportunity. For the determination of linkages between populations and dispersal potentials, for the evaluation of a species' genetic diversity and for the supply of further insights into former and recent population structures and gene flow of certain species, molecular markers were shown providing an expedient alternative (Elbrecht et al. 2014).

SDMs are based on data on single species. In terms of river assessment modelling species abundances, biodiversity or entire macroinvertebrate communities offer the opportunity to directly model specific metrics and thus the ecological status. As an alternative to species-specific models, community models can be used to model either the collective properties of the biota (Ferrier 2002) or to make predictions for individual species from a community model in which information for a wider set of species (for example taxonomic orders or guilds) is used to construct a context in which individual species distributions are described (Barry & Elith 2006). With respect to the Water Framework Directive (European Commission 2000), community models would also provide future applications in river assessment when spatial or temporal changes in stream macroinvertebrate communities (e.g. river restoration activities) are expected. River restorations should preferably be implemented in accessible distance of source populations to build stepping stones for dispersing species (Januschke 2014). Thus, SDMs may significantly contribute to the identification of potential populations within entire river catchments closing gaps of the knowledge about species occurrences.

In conclusion, the studies in this thesis underline the current limitations of modelling stream macroinvertebrate distributions at a regional scale to detect potential populations, especially highlighting the importance of environmental predictors, appropriate validation and species prevalence.

7 Deutsche Zusammenfassung

7.1 Hintergrund

In den letzten 20 Jahren haben artspezifische Verbreitungsmodelle (Species distribution models, SDM) in verschiedenen wissenschaftlichen Gebieten Einzug gehalten. Die Anwendung solcher Modelle ermöglicht es, Habitatpräferenzen einzelner Arten zu bestimmen und das Vorkommen dieser Arten basierend auf den Art-Habitat-Beziehungen vorherzusagen. So werden SDMs beispielsweise im Naturschutz angewendet, um Informationen zur Habitatverfügbarkeit in unbekannten Gebieten zu generieren oder Risiken für gefährdete Arten abzuschätzen (Ferrier 2002, Wilson et al. 2011, Degerman et al. 2013, Prié et al. 2014). Hier können Modelle dazu beitragen, schutzwürdige Gebiete zu erkennen und auszuweisen und ein Risikomanagement für solche Schutzgebiete zu implementieren. Des Weiteren wurden SDMs intensiv dafür verwendet, Auswirkungen des Klimawandels auf Arten zu bestimmen und in die Zukunft zu projizieren (Neilson et al. 1992, Pearson & Dawson 2003, Thomas et al. 2004, Botkin et al. 2007, Buisson & Grenouillet 2009, Domisch et al. 2013a), um somit die Anfälligkeit von Ökosystemen durch den Klimawandel und damit einhergehende Änderungen in der Landnutzung abzuschätzen (Petersen et al. 2002, Pearson & Dawson 2003, Thuiller et al. 2005a, Domisch et al. 2011, 2013, Arribas et al. 2012, Kusch 2015). Darüber hinaus wurden SDMs eingesetzt, um potentielle Auswirkungen globaler Umweltveränderungen (Richardson & Whittaker 2010), anthropogener Stressoren wie Verschmutzung (Tang et al. 2010, Luoto 2011) oder Änderungen in der Landnutzung (Lohse et al. 2008, Kristensen et al. 2012, Kopp et al. 2012) vorherzusagen.

Eine der Hauptfragestellungen in der Ökologie ist, wie und in welchem Ausmaß sich das Artvorkommen oder die Zusammensetzung von Lebensgemeinschaften entlang eines Umweltgradienten verändert. Basierend auf dem Nischenkonzept nach Hutchinson (1957) stellen SDMs das Artvorkommen mit Umweltvariablen und/oder räumlichen Charakteristika statistisch in Zusammenhang. Sie beschreiben demnach die realisierte Nische einer Art. In einem weiteren Schritt projizieren SDMs das potentielle Artvorkommen basierend auf den definierten Art-Umwelt-Beziehungen auf verschiedenen räumlichen Skalen. Dabei ist es möglich, je nach Zielsetzung und Methode, die Habitatverfügbarkeit, Abundanzen, physiologische oder demografische Raten vorherzusagen. Methodisch gesehen wird ein Modell mit Umweltvariablen und binären abhängigen Daten (Präsenz/Absenz von Arten) trainiert und kalibriert. Das beste Modell wird anhand von verschiedenen Maßen (z.B.

Bestimmtheitsmaß) ausgewählt, um die Habitatverfügbarkeit bzw. das Artvorkommen räumlich oder zeitlich vorherzusagen. Daraus resultiert eine Karte, die das potentielle Vorkommen von Arten auch für nicht observierte Regionen visualisiert. Um die Vorhersagequalität eines Modells zu bestimmen, werden die Vorhersagen mit den in die Modelle eingegangen abhängigen Variablen anhand eines Resubstitutionsverfahrens verglichen (Kreuzvalidierung). Zudem können die Vorhersagen auch mit zusätzlichen Daten, die nicht für die Entwicklung der Modelle verwendet wurden, validiert werden, z.B. mit Monitoringdaten oder zusätzlich erhobenen Daten. Durch die Anwendung von SDMs können demnach kontinuierliche räumliche Information zu Arten generiert werden, ohne der Notwendigkeit einer großflächigen, zeit- und ressourcenaufwendigen Datenerhebung.

Neben dem wissenschaftlichen Einsatz werden SDMs in der politischen Anwendung und Umsetzung noch kritisch gesehen aufgrund ihrer vereinfachten Annahmen und daraus resultierenden Grenzen (Zurell et al. 2009, Araújo & Peterson 2012). Besonders die Anwendung in Fließgewässern als eines der heterogensten Ökosysteme auf kleinen Skalen (Erös & Schmera 2010) stellt SDMs vor besondere Herausforderungen. Flüsse und Bäche stellen uni-direktionale und hoch strukturierte Netzwerke dar, die sowohl longitudinal als auch lateral und vertikal miteinander verbunden sind (Ward 1989, Linke et al. 2008). Umweltbedingungen und ökologische Prozesse an oberhalb gelegenen Bereichen als auch in den angrenzenden Einzugsgebieten wirken sich auf die lokalen Bedingungen aus (Allan 2004, Allen & Vaughn 2010, Jähnig et al. 2012). Die Struktur von Habitaten und somit das Vorkommen von Arten werden durch ein komplexes und verschachteltes Zusammenwirken von Umweltfaktoren auf verschiedenen Skalen beeinflusst: von der Oberflächenstruktur eines einzelnen Steins bis hin zum gesamten Einzugsgebiet eines Flusses (Vaughan et al. 2009).

Nachdem sich die Wasserqualität in den Oberflächengewässern in den letzten Jahrzehnten verbessert hat, sind die Auswirkungen von Degradation und der ufernahen Landnutzung auf die Biodiversität und das Artvorkommen in Fließgewässern zu Tage getreten. Durch Uferbegradigungen, Veränderungen des Abflusses durch Querbauwerke oder Ausleitungen und der Zunahme von Landwirtschaft und verbauten Flächen in ufernahen Bereichen sind Habitate für Fließgewässer-Organismen erheblich fragmentiert oder zerstört worden. Hier setzt die Europäische Wasserrahmenrichtlinie an (2000/60/EC, European Commission 2000), die zum Ziel hat, alle Grund- und Oberflächengewässer bezüglich chemischer, struktureller und biologischer Bedingungen bis zum Jahr 2015 in einen guten ökologischen Zustand zu bringen. Die Bewertung des ökologischen Zustands der Biologie basiert dabei auf Lebensgemeinschaften von Fischen, Makrozoobenthos, aquatischer Makrophyten, Diatomeen und Phytobenthos (Hering et al. 2010). Im Zuge dieser Richtlinie wurde eine Vielzahl an Renaturierungen durchgeführt, die die Verbesserung der Gewässerstruktur und damit der Lebensgemeinschaften zum Ziel haben. Bislang bleiben die erwarteten positiven

Reaktionen der Organismen häufig aus, besonders für das Makrozoobenthos sind oft keine oder nur geringe Effekte feststellbar (Roni et al. 2006, Jähnig et al. 2010, Palmer et al. 2010, Sundermann et al. 2011a). Verschiedene Gründe hierfür wurden diskutiert und beinhalten häufig Stressoren auf Einzugsgebietsebene: landwirtschaftliche Nutzung oder organische Belastung in oberhalb gelegenen Abschnitten (Palmer et al. 2010, Lorenz & Feld 2013, Sundermann et al. 2013) und das Fehlen von Wiederbesiedlungsquellen in der Nähe der renaturierten Abschnitte (Sundermann et al. 2011b, Stoll et al. 2013), aber auch die Länge des renaturierten Abschnitts und längere Zeiträume, die zur Wiederbesiedlung benötigt werden (Lorenz et al. 2009, Bernhardt & Palmer 2011, Parkyn & Smith 2011). In diesem Zusammenhang können Verbreitungsmodelle dazu beitragen, die Habitatverfügbarkeit in renaturierten Abschnitten abzuschätzen, verschiedene Szenarios an Veränderungen in der Hydromorphologie und der Landnutzung in Bezug auf Renaturierungen zu berechnen und potentielle Wiederbesiedlungsquellen in der Umgebung von renaturierten Abschnitten zu bestimmen.

Makroinvertebraten reagieren stark auf lokale Umweltbedingungen wie die Wasserqualität und die Substratverfügbarkeit als auch auf großräumige Bedingungen auf der Skala des Einzugsgebietes. Lokale Umweltvariablen werden vor allem an einzelnen Abschnitten regelmäßig überprüft und sind daher nicht kontinuierlich für alle Abschnitte in einem Flusseinzugsgebiet verfügbar. Für die Anwendung von SDMs, die auf Vorhersagen von Makroinvertebraten abzielen, sind großflächig verfügbare Umweltdaten allerdings unabdingbar. In früheren Studien wurde bereits gezeigt, dass die Landnutzung und die Gewässerstruktur im Einzugsgebiet Einfluss auf das Vorkommen von Makroinvertebraten bzw. die Zusammensetzung der Artgemeinschaft hat (Allan 2004, Jähnig et al. 2009, Death & Collier 2010, Feld 2012, Lorenz & Feld 2013). In dieser Dissertation wurden deshalb SDMs mithilfe von großflächig verfügbaren Landnutzungsdaten und der Gewässerstrukturgüte auf einer Skala von 100 m-Abschnitten entwickelt und deren Anwendbarkeit und Vorhersagequalität getestet. Dafür wurden verschiedene Umweltvariablen (Gewässerstrukturgüte, Landnutzung, Physikochemie, Substrate) als auch das Vorkommen von elf ausgewählten Makroinvertebraten in zwei Probenahmezeiträumen (Frühjahr 2010 und 2011, insgesamt 225 Probestellen) in einem Einzugsgebiet im Mittelgebirge (Ruhr, Nordrhein-Westfalen) erhoben. Die SDMs wurden basierend auf großräumig verfügbaren Umweltvariablen (Gewässerstruktur und ufernahe Landnutzung) entwickelt und validiert.

Die folgenden Zielsetzungen und Hypothesen (H) lagen dieser Dissertation zugrunde:

1. Die detaillierte Beschreibung der aktuellen Verbreitung der Makroinvertebraten-Arten und deren ökologische Ansprüche (Kapitel 3)

2. Die Überprüfung der Anwendbarkeit von Verbreitungsmodellen für Makroinvertebraten basierend auf großräumig vorhandenen Umweltvariablen und deren Vergleich mit Modellen basierend auf kleinräumigen Umweltvariablen (Kapitel 4)

   H2a: SDMs, die auf großräumig vorhandenen Umweltvariablen stellvertretend für lokale (kleinräumige) Umweltbedingungen basieren, erreichen eine akzeptable Modellgüte.

   H2b: Die Berücksichtigung von lokalen (kleinräumigen) Umweltvariablen wie Physikochemie und Substraten führt zu einer signifikanten Verbesserung der Modellgüte.

3. Die Überprüfung der Übertragbarkeit von Verbreitungsmodellen für Makroinvertebraten zwischen benachbarten Flusseinzugsgebieten (Kapitel 4)

   H3: Modellvorhersagen für benachbarte Einzugsgebiete, die auf denselben Umweltvariablen basieren, sind untereinander räumlich übertragbar aufgrund ähnlicher Umweltbedingungen.

4. Die Validierung von Verbreitungsmodellen für Makroinvertebraten basierend auf verschiedenen Datensätzen (Kapitel 5)

   H4: Die Validierung von SDMs anhand eines neu erhobenen Datensatzes (Feldvalidierung) erzielt eine realistischere Einschätzung der Vorhersagequalität als eine Kreuzvalidierung oder eine unabhängige Validierung durch Monitoringdaten.

5. Die Untersuchung des Einflusses der Artprävalenz (Frequenz) auf die Güte der Modelle

   H5: SDMs seltener Arten tendieren dazu, Absenzen der Art häufiger vorherzusagen als Präsenzen der Art.

Dem ersten Ziel dieser Dissertation ist eine deskriptive Studie gewidmet, in der die aktuelle Verbreitung der elf ausgewählten Makroinvertebraten, deren Substratpräferenzen und ökologische Ansprüche hinsichtlich der ufernahen Landnutzung, der Parameter der Gewässerstrukturgüte und der Physikochemie beschrieben werden (Kapitel 3). Die Ziele 2 und 3 wurden im Kapitel 4 untersucht. Hierfür wurden Verbreitungsmodelle basierend auf großskaligen Variablen entwickelt und mit solchen verglichen, die zusätzlich kleinräumige Variablen (Physikochemie und Substrate) als Deskriptoren berücksichtigten. Die räumliche

Übertragbarkeit der Modelle wurde getestet, indem die Modelle eines Einzugsgebiets für Vorhersagen im angrenzenden Einzugsgebiet verwendet wurden. Dafür wurde der Datensatz räumlich in zwei Einzugsgebiete (Lenne und obere Ruhr) aufgeteilt und die Vorhersagen für das jeweils andere Einzugsgebiet überprüft. Um die Verbreitungsmodelle zuverlässig zu validieren (Ziele 4 und 5), wurde der Datensatz in einem nächsten Schritt zeitlich aufgeteilt (2010 und 2011). Auf Basis des 2010er Datensatzes wurden SDMs entwickelt, die anhand eines neu und mit gleichen Methoden erhobenen Datensatzes (2011) validiert wurden (Kapitel 5). Die Maße für die Vorhersagequalität aus dieser Feldvalidierung wurden mit denen aus einer Kreuzvalidierung und einer unabhängigen Validierung mit Monitoringdaten verglichen.

Im Folgenden werden die drei Studien, die Vorgehensweisen, die wichtigsten Ergebnisse sowie die Erkenntnisse im Hinblick auf die Hypothesen dargestellt.

7.2 Präferenzen der Arten

Makroinvertebraten sind eine weit verbreitete und hoch diverse Gruppe von aquatischen Organismen, die sowohl stehende als auch fließende Oberflächengewässer besiedeln. Da sie sowohl auf Veränderungen der Wasserqualität als auch der Hydromorphologie und der Landnutzung reagieren, stellen sie eine wichtige Organismengruppe für die Bewertung von Oberflächengewässern in Europa dar. In dieser Dissertation wurden elf Arten aus verschiedenen Ordnungen ausgewählt, die unterschiedliche Lebenszyklen, Ernährungstypen, Verbreitungsmuster und spezifische Präferenzen bezüglich ihres Lebensraums aufweisen. Generell wurden keine starken Zusammenhänge zwischen dem Artvorkommen und Variablen der Landnutzung, Gewässerstrukturgüte, Mesohabitate (Substrate) und Physikochemie gefunden. Allerdings konnte gezeigt werden, dass die Präsenz/Absenz der Arten sich entlang der Gradienten bestimmter Umweltvariablen signifikant unterscheidet. Die ökologischen Ansprüche der Arten werden in diesem Kapitel ausführlich beschrieben und mit Literaturangaben verglichen.

Hydropsyche instabilis war die häufigste Art im Untersuchungsgebiet (52%) während *Hydropsyche incognita* mit einer Prävalenz von 8% die seltenste Art war. Eine Karte der Artvorkommen visualisierte artspezifische Verbreitungsmuster in der Region. In den südlichen Lenne-Zuflüssen (oberhalb der Bigge-Mündung) kamen nahezu keine der elf Modellarten vor. Dies weist auf eine frühere Verschmutzung, Versauerung und degradierte Hydromorphologie hin, wodurch diese Abschnitte nicht wiederbesiedelt werden konnten. Im Gegensatz dazu kamen in der Quellregion der Lenne und der Ruhr im Vergleich zu den unterhalb gelegenen Abschnitten die meisten Arten gleichzeitig vor. Dies weist auf eine Wiederbesiedlung der Lenne durch die benachbarten Ruhr-Zuflüsse hin.

Ziel 1 *Die detaillierte Beschreibung der aktuellen Verbreitung der Makroinvertebraten-Arten und deren ökologische Ansprüche* wurde erfüllt.

Schlussfolgerung:

Groß- und kleinräumige Umweltvariablen wurden detailliert an insgesamt 225 Probestellen erhoben. Demnach stand ein hochwertiger Datensatz an Umweltvariablen und dazugehörigen binären Daten zu Präsenz/Absenz der Arten zur weiteren Auswertung zur Verfügung. Die Umweltvariablen konnten artspezifisch mit dem Vorkommen in Zusammenhang gebracht werden und somit die Habitatpräferenzen der Arten adäquat beschrieben werden. Diese Profile tragen zum Verständnis der Verbreitungsmuster und potentieller Populationen in diesem Untersuchungsgebiet bei.

7.3 SDMs basierend auf großräumigen Umweltvariablen und deren Übertragbarkeit

Makroinvertebraten besiedeln kleinräumige Habitate auf Skalen von cm bis einige Quadratmeter. Des Weiteren wird die Verbreitung von Makroinvertebraten auch von großräumigen Umweltbedingungen, wie z.B. die Landnutzung in oberhalb gelegenen Flussabschnitten, beeinflusst. Lokale Umweltvariablen sind meistens nicht kontinuierlich und für das gesamte Einzugsgebiet verfügbar, sodass die Anwendung von Verbreitungsmodellen auf regionalen Skalen limitiert ist. In dieser Studie wurden Verbreitungsmodelle auf großräumig verfügbaren Daten zu Landnutzung (ATKIS) und Hydromorphologie (Gewässerstrukturgütekartierung) entwickelt. Daten zur Präsenz/Absenz der elf Makroinvertebraten-Arten in zwei benachbarten Teileinzugsgebieten im Mittelgebirge (Lenne und obere Ruhr) wurden durch eine umfangreiche Probenahme erhoben. Für beide Teileinzugsgebiete wurden separat SDMs entwickelt. Dafür wurde eine nicht-parametrische multiplikative Regressionsmethode (NPMR) angewendet. Um die Anwendbarkeit von großräumigen Umweltvariablen für die Verbreitungsmodellierung zu überprüfen, wurden verschiedene Maße zur Beschreibung der Güte (logB) und Vorhersagequalität (AUC) der Modelle herangezogen. Zudem wurden die Modellergebnisse mit solchen SDMs verglichen, die zusätzlich lokal verfügbare, kleinräumige Umweltvariablen (Physikochemie und Substrate) berücksichtigten. In einem dritten Schritt wurde die Übertragbarkeit der SDMs zwischen Lenne und Ruhr anhand eines Indexes (transferability index) untersucht. Aufgrund ähnlicher Umweltgradienten in beiden Teileinzugsgebieten wurde eine Übereinstimmung der SDMs zwischen Lenne und Ruhr erwartet.

Für die Steinfliegenart *Dinocras cephalotes* wurden zuverlässige Modelle für beide Teileinzugsgebiete gefunden. Für einige Arten zeigten die Modelle moderate Ergebnisse im Ruhr-Einzugsgebiet, allerdings nicht im Lenne-Einzugsgebiet (*Leuctra geniculata, Silo piceus, Siphlonurus lacustris*). Für *Hydropsyche instabilis* zeigte das Modell für die Lenne eine bessere Güte als für die Ruhr. Sowohl Landnutzungsanteile als auch hydromorphologische Variablen wurden von den Modellen im gleichen Maße als Prädiktoren berücksichtigt. Für fünf von elf Arten übertraf die Qualität der Modelle, die zusätzlich kleinräumige Umweltvariablen einbezogen, solche, die ausschließlich auf großräumigen Umweltvariablen basierten (AUC > 0.70). Diese Arten waren vorrangig in quellnäheren Gewässerabschnitten zu finden. Solche Arten reagieren eindeutiger auf kleinräumige Umweltbedingungen wie Substrate und Physikochemie aufgrund der stärkeren Abhängigkeit ihres Vorkommens von lokalen Umweltbedingungen. Die Vorhersagequalität des Modells von *Hydropsyche incognita* war im Gegensatz zur Modellgüte sehr hoch, was auf einen Zusammenhang zwischen Vorhersagequalität und Artprävalenz, besonders für seltene Arten, hindeutet. Die SDMs ließen sich nur in begrenztem Maße auf das jeweils andere Teileinzugsgebiet übertragen (transferability index < 0.60). Die Modellgüte und Vorhersagequalität der SDMs variierten demnach nicht nur zwischen den Arten, sondern auch zwischen benachbarten Teileinzugsgebieten. Die Übertragbarkeit der Modelle scheint sowohl durch aktuelle als auch historische Unterschiede in den Umweltgradienten beider Teileinzugsgebiete limitiert zu sein. Dies beeinflusst die Verbreitung der Arten bis heute.

Diese Studie war den Zielen 2 und 3 gewidmet:

2. Die Überprüfung der Anwendbarkeit von Verbreitungsmodellen für Makroinvertebraten basierend auf großräumig vorhandenen Umweltvariablen und deren Vergleich mit Modellen basierend auf kleinräumigen Umweltvariablen

   H2a: SDMs, die auf großräumig vorhandenen Umweltvariablen stellvertretend für lokale (kleinräumige) Umweltbedingungen basieren, erreichen eine akzeptable Modellgüte.

   - Die Hypothese wird durch die Ergebnisse teilweise unterstützt. Die Modellgüten variierten zwischen den Arten und Teileinzugsgebieten.

   H2b: Die Berücksichtigung von lokalen (kleinräumigen) Umweltvariablen wie Physikochemie und Substraten führt zu einer signifikanten Verbesserung der Modellgüte.

- Die Hypothese wird durch die Ergebnisse teilweise unterstützt. Für einige Arten war eine Verbesserung der Modellgüte erkennbar, im Allgemeinen war diese nicht signifikant.

3. Die Überprüfung der Übertragbarkeit von Verbreitungsmodellen für Makroinvertebraten zwischen benachbarten Flusseinzugsgebieten

   H3: Modellvorhersagen für benachbarte Einzugsgebiete, die auf denselben Umweltvariablen basieren, sind untereinander räumlich übertragbar aufgrund ähnlicher Umweltbedingungen.

   - Die Hypothese wurde durch die Ergebnisse nicht gestützt.

Schlussfolgerungen:

Die SDMs basierend auf großräumigen Umweltvariablen zur ufernahen Landnutzung und Gewässerstruktur zeigten im Allgemeinen einen moderaten bis schwachen Art-Umwelt-Zusammenhang an. Die Berücksichtigung von lokalen, kleinräumigen Umweltvariablen wie Substratanteile und Physikochemie führten nicht zu einem erheblichen Anstieg der Modellqualitäten. Dies weist darauf hin, dass solche Umweltfaktoren, die wesentlich das Vorkommen der betrachteten Arten bestimmen, nicht in den Modellen berücksichtigt wurden.

Diese Studie bestätigt zudem, dass SDMs nicht allgemein gültig sind, sondern auch in benachbarten Regionen zu unterschiedlichen Ergebnissen und Vorhersagen führen können. Die zugrunde liegenden Umweltgradienten in den jeweiligen Untersuchungs-gebieten und die Übertragbarkeit von SDMs zwischen Regionen müssen daher hinreichend überprüft werden. Bezüglich einer potentiellen Anwendung von SDMs in der Gewässerbewertung und der Abschätzung des Renaturierungserfolges sind demnach weiterführende Untersuchungen zur Übertragung von Modellvorhersagen zum Vorkommen von Makroinvertebraten nötig.

Obwohl die in dieser Studie entwickelten Verbreitungsmodelle aufgrund ihrer teilweise schwachen Qualitäten keine Anwendung in Umweltschutzmaßnahmen finden werden, geben die Ergebnisse einen wertvollen Einblick in die Komplexität und die Grenzen von SDMs, die auf großräumigen Umweltvariablen basieren.

7.4 Validierung der SDMs

Die Qualität eines Modells wird durch ein Bestimmtheitsmaß (hier pseudo-R2) wiedergegeben das die Stärke des Zusammenhangs zwischen Artvorkommen und Umweltvariablen angibt. Dies gibt jedoch keinen Aufschluss darüber, wie verlässlich ein Modell die Präsenz bzw. Absenz der Arten prognostiziert. Die Validierung zielt darauf ab, die Richtigkeit der vorhergesagten Präsenzen und Absenzen der Arten zu überprüfen, indem die Vorhersagen mit reellen Präsenzen/Absenzen der Arten verglichen werden. In dieser Studie wurden SDMs für die elf Arten basierend auf dem Datensatz des Jahres 2010 entwickelt. Hierfür wurden zwei statistische Methoden angewendet: die nicht-parametrische multiplikative Regression und die logistische Regression. Als Umweltvariablen wurden ufernahe Landnutzungsanteile und Parameter der Gewässerstrukturgüte herangezogen. Die Vorhersagen der Modelle wurden anhand von drei verschiedenen Datensätzen validiert: i) eine Kreuzvalidierung mit den binären Daten, die bereits in die Entwicklung des SDMs eingegangen sind (unter Anwendung eines Resubstitutionsverfahrens, 121 Probestellen), ii) eine Validierung mit unabhängig erhobenen Daten zum Artvorkommen (Monitoringdaten, 620 Probestellen) und iii) eine Feldvalidierung mit einem neu erhobenen Datensatz (2011, 104 Probestellen). Die Probenahme im Jahr 2011 zielte darauf ab, die Modellvorhersagen für die einzelnen Arten unter Anwendung derselben Besammlungsmethoden im Feld zu überprüfen, d.h. hier wurde ein abhängiger Datensatz mit gleicher Auflösung verwendet. Für die unterschiedlichen Validierungsmethoden wurden verschiedene Maße der Vorhersagequalität berechnet (AUC, PCC, TSS und Anteile an korrekt vorhergesagten Präsenzen und Absenzen) und in Abhängigkeit von der Prävalenz (Häufigkeit) der Arten dargestellt. Zudem wurde der Zusammenhang zwischen Modellgüte und Vorhersagequalität eines Modells präsentiert.

Für die Plecopterenart *Dinocras cephalotes* und die Trichopteren *Silo piceus* und *Silo pallipes* wurden akzeptable Modellgüten erreicht. Die Maße der Modellgüte und der Vorhersagequalität eines SDMs waren nicht miteinander korreliert. Demnach lässt eine gute Modellgüte nicht automatisch auf eine gute Vorhersagequalität des Modells schließen. Die Kreuzvalidierung zeigte deutlich höhere Vorhersagequalitäten im Vergleich zur Feldvalidierung und unabhängigen Validierung. Dies zeigt, dass die Kreuzvalidierung aufgrund des internen Vergleichs der Vorhersagen mit korrelierten Artvorkommen die Vorhersagequalität eines Modells deutlich überschätzt. Die Maße der Vorhersage-qualitäten (AUC, TSS) nahmen im Mittel von der Kreuzvalidierung über die Feldvalidierung zur unabhängigen Validierung hin ab. Die Maße der unabhängigen Validierung zeigten die niedrigsten Vorhersagequalitäten an. Hierfür werden unterschiedliche Probenahmedesigns und Saisonalität als Ursachen diskutiert. Die Feldvalidierung als abhängige, aber direkte Überprüfung der Vorhersagen im Feld bietet eine gute Alternative zur Abschätzung der realen Vorhersagegüte. Die Prävalenz der Arten lag zwischen 8 und 50% im Untersuchungsgebiet und hatte einen deutlichen Einfluss auf

bestimmte Maße der Vorhersagequalität. Während AUC und TSS unabhängig von der Prävalenz waren, wurde für PCC und die Anteile an korrekt vorhergesagten Präsenzen und Absenzen einen deutlicher Zusammenhang mit der Prävalenz nachgewiesen. Insgesamt tendierten SDMs seltenerer Arten dazu, häufiger Absenzen als Präsenzen vorherzusagen. Die Anwendung genereller Gütekriterien für SDMs kann demnach zu Fehlinterpretationen führen, wenn die Prävalenz unbeachtet bleibt.

Diese Studie war den Zielen 4 und 5 gewidmet:

4. Die Validierung von Verbreitungsmodellen für Makroinvertebraten basierend auf verschiedenen Datensätzen (Kapitel 5)

   H4: Die Validierung von SDMs anhand eines neu erhobenen Datensatzes (Feldvalidierung) erzielt eine realistischere Einschätzung der Vorhersagequalität als eine Kreuzvalidierung oder eine unabhängige Validierung durch Monitoringdaten.

   - Die Hypothese wurde durch die Ergebnisse gestützt.

5. Die Untersuchung des Einflusses der Artprävalenz (Frequenz) auf die Güte der Modelle

   H5: SDMs seltener Arten tendieren dazu, Absenzen der Art häufiger vorherzusagen als Präsenzen der Art.

   - Die Hypothese wurde durch die Ergebnisse gestützt.

<u>Schlussfolgerungen:</u>

Wie auch schon in der vorherigen Studie wiesen die SDMs, die mit großräumigen Umweltvariablen trainiert wurden, eine moderate Modellgüte auf. Dies deutet darauf hin, dass die Verwendung von großräumigen Umweltvariablen wichtige Faktoren, die die Verbreitung von Makroinvertebraten in diesem Untersuchungsgebiet wesentlich beeinflussen, nicht einbezieht. Zudem müssen die Qualität eines Modells und seine Vorhersagen isoliert voneinander betrachtet werden. Von einem starken Zusammenhang zwischen Art und Umwelt, ausgedrückt als Modellgüte, kann nicht auf die Verlässlichkeit der Modellvorhersagen geschlossen werden. Für SDMs, die die Prognose von Vorkommenswahrscheinlichkeiten einer Art zum Zweck haben, ist es daher unabdingbar sowohl die Modellgüte als auch die Vorhersagequalität präzise zu evaluieren.

Meine Ergebnisse unterstützen andere Studien, die die Tendenz der Kreuzvalidierung zur Überschätzung der Vorhersagequalität nachgewiesen haben (Araújo et al. 2005, Olden & Jackson 2000, 2002). Die SDMs werden auf die vorhandenen Daten und den darin beschriebenen Umweltgradienten optimiert und können dadurch ihre Allgemeingültigkeit außerhalb dieser Gradienten verlieren. Die Feldvalidierung stellt eine Alternative zur Kreuzvalidierung und unabhängigen Validierung dar. Kleine Datensätze müssen nicht weiter aufgeteilt werden, bzw. es werden keine Daten verwendet, die zu einem anderen Zweck erhoben wurden. Dennoch besteht weiterer Forschungsbedarf, um die Umsetzbarkeit einer Feldvalidierung weiter zu entwickeln.

Die Prävalenz einer Art spielt eine wichtige Rolle bei der Entwicklung und Anwendbarkeit von SDMs, da besonders seltene und gefährdete Arten im Fokus von wissenschaftlichen Untersuchungen und Schutzmaßnahmen stehen. Besonders Fließgewässerorganismen mit komplexen Lebenszyklen und ungleichmäßigen Verbreitungsmustern bewohnen ein sehr dynamisches und vielschichtiges Ökosystem. Verschiedene Probenahmezeiträume und –methoden können daher zu einer Unterschätzung der Häufigkeit einer Art in einem Einzugsgebiet führen. Die Berücksichtigung der Prävalenz und deren Auswirkungen auf die Qualität eines Modells sind daher bei der Entwicklung, Beurteilung und Anwendung von SDMs unerlässlich.

7.5 Ausblick

Die Anwendung von Verbreitungsmodellen auf Makroinvertebraten in Fließgewässern hat sich in den letzten Jahren stetig entwickelt. Allerdings ist die Verwendung von großräumigen Umweltvariablen, die eher einen indirekten Einfluss auf die Verbreitung der Arten auf regionalen Skalen haben, als neu anzusehen. Die Ergebnisse dieser Arbeit zeigten die limitierte Verwendbarkeit solcher Umweltvariablen für SDMs und weisen darauf hin, dass entscheidende Faktoren und Prozesse für die Verbreitung von Makroinvertebraten durch die hier verwendeten großräumigen Umweltvariablen (Landnutzung und Gewässerstrukturgüte) nicht berücksichtigt werden. Dennoch führte eine Integrierung von physikochemischen Variablen und Subtraten nicht zu der erwarteten Verbesserung der Modellgüten. Die Modellqualitäten zwischen verschiedenen Arten variierten z.T. stark. Hier besteht weiterer Forschungsbedarf, um sowohl kleinskalige, lokale als auch großräumige (surrogate) Faktoren, die kleinräumige Art-Umwelt-Zusammenhänge adäquat beschreiben, zu definieren. Dies macht es erforderlich, die Autökologie der Arten, ihre aktuellen Verbreitungsmuster und Ausbreitungskapazitäten und -wege weiter intensiv zu untersuchen. Die Lebenszyklen von Makroinvertebraten, vor allem merolimnischer Arten, beinhalten viele verschiedene Stadien (z.B. die richtigen Habitate zur Eiablage, Emergenz und Schwarmverhalten), die

unterschiedliche abiotische und biotische Umweltbedingungen voraussetzen. Die Herausforderung wird sein, im Lebenszyklus einer Art die sensitivsten Stadien zu definieren, die die Verbreitung wesentlich determinieren. Aktuell wurde bei der Deutschen Forschungsgemeinschaft (DFG) ein Antrag für eine Forschergruppe gestellt, die sich zum Ziel gesetzt hat, intrinsische (d.h. morphologische, physiologische und genetische) als auch extrinsische (d.h. Habitatverfügbarkeit, Barrieren für die Ausbreitung, Parasitenbefall) Faktoren zu untersuchen, die die Besiedlung und Etablierung von Arten und taxonomischen Gruppen als wesentliche ökologische Prozesse beeinflussen.

Seit Beginn dieser Dissertation haben sich integrative Modellierungsansätze bewährt, die ökologische und hydrologische Modelle miteinander verknüpfen (Kuemmerlen et al. 2012, 2014). Zudem stellt die Berücksichtigung von dynamischen, biotischen Faktoren wie die Migration in neue Lebensräume (Franklin 2010), die Ausbreitungsfähigkeit der Arten und deren Barrieren, die Distanz zwischen einzelnen Populationen (Sondermann et al. 2015) sowie Dominanzstrukturen in einer Lebensgemeinschaft (le Roux et al. 2014) eine sinnvolle Erweiterung der ansonsten statischen Verbreitungsmodelle dar. Die Ausbreitung der Arten in neue Lebensräume ist eine treibende Kraft für die Wiederbesiedlung, Etablierung und Struktur der Lebensgemeinschaft. Die Verbindung von SDMs mit prozessorientierten Modellen, die die Dynamik der Arten, der Populationen und deren Umwelt hinreichend prognostizieren können, sowie die Integration von Modellen zu Hydrologie, Mesohabitaten und Klima (z.B. Fukuda et al. 2014) ist eine vielversprechende Herausforderung für die zukünftige Modellierung von Fließgewässersystemen. Für die Untersuchung der genetischen Diversität, des Ausbreitungspotenzials einer Art und des Genflusses zwischen Population haben sich molekulare Marker als nützliche Methode erwiesen (Elbrecht et al. 2014).

SDMs modellieren das Vorkommen einzelner Arten. In der Gewässerbewertung ist es jedoch angemessen, Abundanzen oder gesamte Lebensgemeinschaften zu modellieren und sich so die Möglichkeit zu eröffnen, bewertungsrelevante Metrics oder den ökologischen Zustand zu prognostizieren. Sogenannte Community-Modelle können beispielsweise dazu genutzt werden, Eigenschaften kompletter Gemeinschaften wie die Biodiversität, taxonomische Gruppen oder funktionelle Einheiten abzuschätzen (Barry & Elith 2006, Ferrier 2002). Vor dem Hintergrund der Wasserrahmenrichtlinie (European Commission 2000) stellen Community-Modelle eine sinnvolle Anwendung im Gewässermanagement dar, wenn die Reaktion einer Lebensgemeinschaft auf eine hydromorphologische Veränderung, wie beispielsweise eine Renaturierungsmaßnahme, im Fokus steht. Renaturierungen sollten idealerweise in adäquater Distanz zu Quellpopulationen durchgeführt werden, um eine Wiederbesiedlung zu garantieren (Januschke 2014). Hier können Community-Modelle als auch integrative SDMs helfen potentielle Quellpopulationen im Einzugsgebiet zu identifizieren und den Erfolg einer Renaturierung im Hinblick auf den guten ökologischen Zustand langfristig abzuschätzen.

8 References

Acevedo P., González-Quirós P., Prieto J.M., Etherington T.R., Gortázar C. & Balseiro A. (2014) Generalizing and transferring spatial models: A case study to predict Eurasian badger abundance in Atlantic Spain. Ecological Modelling 275, 1-8.

Allan J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. Annual Review of Ecology Evolution and Systematics 35, 257-284.

Allen D.C. & Vaughn C.C. (2010) Complex hydraulic and substrate variables limit freshwater mussel species richness and abundance. Journal of the North American Benthological Society 29, 383-394.

Allouche O., Tsoar A. & Kadmon R. (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). Journal of Applied Ecology 43, 1223-1232.

Andersen M.C., Adams H., Hope B. & Powell M. (2004) Risk analysis for invasive species: general workflow and research needs. Risk Analysis 24, 893-900.

Araújo M.B. & Williams P.H. (2000) Selecting areas for species persistence using occurrence data. Biological Conservation 96, 331-345.

Araújo M.B., Pearson R.G., Thuiller W. & Erhard M. (2005) Validation of species-climate impact models under climate change. Global Change Biology 11, 1504-1513.

Araújo M.B. & Guisan A. (2006) Five (or so) challenges for species distribution modelling. Journal of Biogeography 33, 1677-1688.

Araújo M.B. & Luoto M. (2007). The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16, 743-753.

Araújo M.B. & Peterson A.T. (2012) Uses and misuses of bioclimatic envelope modelling. Ecology 93(7), 1527-1539.

Araújo M.B., Pearson R.G., Thuiller W. & Erhard M. (2005) Validation of species-climate impact models under climate change. Global Change Biology 11, 1504-1513.

Arlot S. & Celisse A. (2010) A survey of cross-validation procedures for model selection. Statistics Surveys 4, 40-79.

Armitage P.D., Moss D., Wright J.F. & Furse M.T. (1983) The performance of a new biological water quality score system based on macroinvertebrates over a wide range of unpolluted running-water sites. Water Research 17, 333-347.

Arribas P., Abellán P., Velasco J., Bilton D.T., Millán A. & Sánchez-Fernández D. (2012) Evaluating drivers of vulnerability to climate change: A guide for insect conservation strategies. Global Change Biology 18(7), 2135-2146.

ATKIS (2007) ATKIS - Objektartenkatalog Basis-DLM. Version 3.2. <http://www.atkis.de>

Austin M.P. (2002) Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecological Modelling 157, 101-118.

Austin M.P., Belbin L., Meyers J.A., Doherty M.D. & Luoto M. (2006) Evaluation of statistical models used for predicting plant species distributions: Role of artificial data and theory. Ecological Modelling 199, 197-216.

Austin M. (2007) Species distribution models and ecological theory: A critical assessment and some possible new approaches. Ecological Modelling 200, 1-19.

Bahn V. & McGill B.J. (2013) Testing the predictive performance of distribution models. Oikos 122, 321-331.

Bailey S.-A., Haines-Young R.H. & Watkins C. (2002) Species presence in fragmented landscapes: modeling of species requirements at the national level. Biological Conservation 108, 307-316.

Barbosa A.M., Real R., Muñoz A.-R. & Brown J.A. (2013) New measures for assessing model equilibrium and prediction mismatch in species distribution models. Diversity and Distributions 19, 1333-1338.

Barbosa A.M., Real R. & Vargas J.M. (2009) Transferability of environmental favourability models in geographic space: The case of the Iberian desman (Galemys pyrenaicus) in Portugal and Spain. Ecological Modelling 220, 747-754.

Barry S. & Elith J. (2006) Error and uncertainty in habitat models. Journal of Applied Ecology 43, 413-423.

Bauernfeind E., Moog O. & Weichselbaumer P. (2002) Ephemeroptera. In: Moog, O. (ed.): Fauna Aquatica Austriaca, Lieferung 2002, Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Bayerisches Landesamt für Wasserwirtschaft (1992) Bestimmungsschlüssel für die Saprobier-DIN-Arten (Makroorganismen). Informationsberichte Heft 2/88, 274pp.

Beisel J.N., Usseglio-Polatera P. & Moreteau J.C. (2000) The spatial heterogeneity of a river bottom: a key factor determining macroinvertebrate communities. Hydrobiologia 422/423, 163-171.

Belfiore C. (1983) Efemerotti (Ephemeroptera). Consiglio Nazionale delle Richerche AQ/1/201. Guide per il riconoscimento delle specie animali delle aque interne Italiane 24. Verona. In: Schmedtje, U. & Colling, M. (1996): Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4/96.

Bellmann H. (1993, 2007) Libellen. Beobachten. Bestimmen. Neumann-Neudamm, Melsungen.

Bellmann H. (2007) Der Kosmos-Libellenführer: Die Arten Mitteleuropas sicher bestimmen. Franckh-Kosmos-Verlag, Stuttgart, 320pp. ISBN: 978-3-440-13516-7

Benedict M., Levine R., Hawley W. & Lounibos L.P. (2007) Spread of The Tiger: Global Risk of Invasion by the Mosquito Aedes albopictus. Vector Borne Zoonotic Dis 7, 76-85.

Bernhardt E.S. & Palmer M.A. (2011) River restoration: the fuzzy logic of repairing reaches to reverse catchment scale degradation. Ecological applications 21, 1926-1931.

Bizzi S., Surridge B.W.J. & Lerner D.N. (2013) Structural Equation Modelling: A novel statistical framework for exploring the spatial distribution of benthic macroinvertebrates in riverine ecosystems. River Research and Application 29, 743-759.

BMU (2013) Imprint: Water Framework Directive - Implementation of WFD programs of measures - interim results 2012. 36pp.

Botkin D.B., Saxe H., Araújo M.B., Betts R., Bradshaw R.H.W., Cedhagen, T., Chesson P., Dawson, T.P., Etterson J.R., Faith D.P., Ferrier S., Guisan A., Skjoldborg Hansen A., Hilbert D.W., Loehle C., Margules C., New M., Sobel M.J. & Stockwell D.R.B. (2007) Forecasting the Effects of Global Warming on Biodiversity. BioScience 57, 227-236.

Boyero L. (2003) The quantification of local substrate heterogeneity in streams and its significance for macroinvertebrate assemblages. Hydrobiologia 499(1-3), 161-168.

Brinkhurst R.O. (19749 The Bentlzos of Lakes. St. Martin's Press, New York.

Brotons L., Thuiller W., Araújo M.B. & Hirzel A.H. (2004) Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27, 437-448.

Brown J.H., Mehlman D.W. & Stevens G.C. (1995) Spatial variation in abundance. Ecology 76, 2028-2043.

Buffagni A., Cazzola M., López-Rodríguez M.J., Alba-Tercedor J. & Armanini D.G. (2009) Distribution and Ecological Preferences of European Freshwater Organisms. Volume 3 - Ephemeroptera. Edited by Schmidt-Kloiber, A. & D. Hering. Pensoft Publishers (Sofia-Moscow). 254pp.

Buisson L. & Grenouillet G. (2009) Contrasted impacts of climate change on stream fish assemblages along an environmental gradient. Diversity and Distributions 15, 613-626.

Bunn S.E., P.M. Davies & Mosisch T.D. (1999) Ecosystem measures of river health and their response to riparian and catchment degradation. Freshwater Biology 41, 333-345.

Burgmer T., Hillebrand H. & Pfenninger M. (2007) Effects of climate-driven temperature changes on the diversity of freshwater macroinvertebrates. Oecologia 151, 93-103.

Burmeister H. (1992) Trichoptera. Informationsbericht des Bayerischen Landesamts für Wasserwirtschaft 2/88, 185-227. 2. Überarbeitete Auflage, München.

Cantor S.B., Sun C.C., Tortolero-Luna G., Richards-Kortum R., & Follen M. (1999) A comparison of C/B ratios from studies using receiver operating characteristic curve analysis. Journal of Clinical Epidemiology 52, 885-892.

Caspers N. & Stiers H. (1977) Beitrag zur Kenntnis der Plecopteren der Eifel (Insecta: Plecoptera). Decheniana 130, 136-150, Bonn.

Cicchetti D.V. & Feinstein A.R. (1990) High agreement but low kappa. II. Resolving the paradoxes. Journal of Clinical Epidemiology 43, 551-558.

Clements W.H., Vieira N.K.M. & Church S.E. (2010) Quantifying restoration success and recovery in a metal-polluted stream: a 17-year assessment of physicochemical and biological responses. Journal of Applied Ecology 47, 899-910.

Cohen J. (1960) A coefficient of agreement for nominal scales. Educational and Psychological Measurement 20, 37-46.

Collier K.J. (2008) Temporal patterns in the stability, persistence and condition of stream macroinvertebrate communities: relationships with catchment land-use and regional climate. Freshwater Biology 53(3), 603-616.

Covich A.P., Palmer M.A., & Crowl T.A. (1999) The role of benthic invertebrate species in freshwater ecosystems: zoobenthic species influence energy flows and nutrient cycling. BioScience 49(2), 119-127.

Culp J.M., Walde S.J., & Davies R.W. (1983) Relative importance of substrate particle size and detritus to stream benthic macroinvertebrate microdistribution. Canadian Journal of Fisheries and Aquatic Sciences 40(10), 1568-1574.

De Araújo C.B., Marcondes-Machado L.O. & Costa G.C. (2014) The importance of biotic interactions in species distribution models: a test of the Eltonian noise hypothesis using parrots. Journal of Biogeography 41, 513-523.

Death R.G. & Collier K.J. (2010) Measuring stream macroinvertebrate responses to gradients of vegetation cover: when is enough? Freshwater Biology 55, 1447-1464.

Death R.G. & Collier K.J. (2010) Measuring stream macroinvertebrate responses to gradients of vegetation cover: when is enough enough? Freshwater Biology 55(7), 1447-1464.

Degerman E., Andersson K., Söderberg H., Norrgrann O., Henrikson L., Angelstam P. & Törnblom J. (2013) Predicting population status of freshwater pearl mussel (*Margaritifera margaritifera*, L.) in central Sweden using instream and riparian zone land-use data. Aquatic Conservation: Marine and Freshwater Ecosystems 23(2), 332-342.

DeRolph C.R., Nelson S.A.C, Kwak T.J. & Hain E.F. (2015) Predicting fine-scale distributions of peripheral aquatic species in headwater streams. Ecology and Evolution 5(1), 152-163.

Despax R. (1951) Faune de France 55. Plécoptères. P. Lechevalier, Paris, 280pp.

Domisch S. (2012) Species distribution modelling of stream macroinvertebrates under climate change scenarios. PhD thesis, 81pp.

Domisch S., Jähnig S.C. & Haase P. (2011) Climate-change winners and losers: Stream macroinvertebrates of a submontane region in Central Europe. Freshwater Biology 56(10), 2009-2020.

Domisch S., Araújo M.B., Bonada N., Pauls S.U., Jähnig S.J. & Haase P. (2013a) Modelling distribution in European stream macroinvertebrates under future climates. Global Change Biology 19, 752-762.

Domisch S., Kuemmerlen M., Jähnig S.C. & Haase P. (2013b) Choice of study area and predictors affect habitat suitability projections, but not the performance of species distribution models of stream biota. Ecological Modelling 257, 1-10.

Domisch S., Jähnig S.C., Simaika J.P., Kuemmerlen M. & Stoll S. (2015) Application of species distribution models in stream ecosystems: the challenge of spatial scale, environmental predictors and species occurrence data. Fundamental and Applied Limnology, in press.

Dray S. & Dufour A.B. (2007) The ade4 package: implementing the duality diagram for ecologists. – Journal of Statistical Software 22(4), 1-20.

Durance I. & Ormerod S.J. (2007) Climate change effects on upland stream macroinvertebrates over a 25-year period. Global Change Biology 13, 942-957.

Eder E., Hödl W., Moog O., Nesemann H., Pöckl M. & Wittmann K. (1995) Crustacea (authors depending on taxagroup). In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschafft, Wien.

Edington J.M. & Hildrew A.G. (1981) A key to the caseless caddis larvae of the British Isles: with notes on their ecology (No. 43). Ambleside: Freshwater Biological Association, 92pp.

Edington J.M. & Hildrew A.G. (1995) Caseless caddis larvae of the British Isles (with notes on their ecology). Freshwater Biological Association Scientific Publication No. 53.

Eggers T.O. & Martens A. (2004) Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands. Lauterbornia 42, 68pp.

Eggers T.O. & Martens A. (2007) Ergänzungen und Korrekturen zum "Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands". Lauterbornia 50, 1-13.

Eiseler B. & Enting K. (2010) Verbreitungsatlas der Steinfliegen (Plecoptera) in Nordrhein-Westfalen. Band 23 von LANUV-Fachbericht, Nordrhein-Westfalen Landesamt für Natur, Umwelt und Verbraucherschutz, 177pp.

Eiseler B. (2005) Bildbestimmungsschlüssel für die Eintagsfliegenlarven der deutschen Mittelgebirge und des Tieflands. Lauterbornia 53, 112pp.

Elbrecht V., Feld C.K., Gies M., Hering D., Sondermann M., Tollrian R., & Leese F. (2014) Genetic diversity and dispersal potential of the stonefly Dinocras cephalotes in a central European low mountain range. Freshwater Science 33(1), 181-192.

Elith J., Graham C.H., Anderson R.P., Dudík M., Ferrier S., Guisan A., Hijmans R.J., Huettmann F., Leathwick J.R., Lehmann A., Li J., Lohmann L.G., Loiselle B.A., Manion G., Moritz C., Nakamura M., Nakazawa Y., Overton J. McC., Peterson A.T., Phillips S.J., Richardson K.S., Scachetti-Pereira R., Schapire R.E., Soberón J., Williams S., Wisz M.S. & Zimmermann N.E. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129-151.

Elith J. & Leathwick J.R. (2009) Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology Evolution and Systematics 40, 677-697.

Elliott J.M. (1987) Life cycle and growth of Leuctra geniculata (Stephens) (Plecoptera: Leuctridae) in the River Leven. Entomologist's Gazette 38, 129-134.

Elliott J.M., Humpesch U.H. & Macan T.T. (1988) Larvae of the British Ephemeroptera: a key with ecological notes (No. 49). Freshwater Biological Association Scientific Publications 49, 141pp., Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Elliott J.M. (2005) Day–night changes in the spatial distribution and habitat preferences of freshwater shrimps, *Gammarus pulex*, in a stony stream. In: Freshwater Biology (2005) 50, 552-566.

Erös T. & Schmera D. (2010) Spatio-temporal scaling of biodiversity and the species-time relationship in a stream fish assemblage. Freshwater Biology 55, 2391-2400.

Ervin G.N. & Holly D.C. (2011) Examining Local Transferability of Predictive Species Distribution Models for Invasive Plants: An Example with Cogongrass (Imperata cylindrica). Invasive Plant Science and Management 4(4), 390-401.

Eskildsen A., le Roux P.C., Heikkinen R.K., Høye T.T., Kissling W.D., Pöyry J., Wisz M.S. & Luoto M. (2013) Testing species distribution models across space and time: High latitude butterflies and recent warming. Global Ecology and Biogeography 22, 1293-1303.

ESRI (2011) ArcGIS Desktop: Release 10.0. Redlands, CA: Environmental Systems Research Institute. <www.esri.com>

ESRI (2011) ArcGIS Desktop: Release 9.3. Redlands, CA: Environmental Systems Research Institute. <www.esri.com>

European Commission (2000) Directive 2000/60/EC, Establishing a framework for community action in the field of water policy. Official Journal of the European Communities L327, 71pp., Brussels, Belgium.

Evangelista P.H., Kumar S., Stohlgren T.J., Jarnevich C.S., Crall A.W., Norman III J.B., & Barnett D.T. (2008) Modelling invasion for a habitat generalist and a specialist plant species. Diversity and Distributions 14, 808-817.

Fawcett T. (2006) An introduction to ROC analysis. Pattern Recognition Letters 27, 861-874.

Feld C.K. (2004) Identification and measure of hydromorphological degradation in Central European lowland streams. Hydrobiologia, 516, 69-90.

Feld C.K., Birk S., Bradley D.C., Hering D., Kail J., Marzin A., Melcher A., Nemitz D., Pedersen M.L., Pletterbauer F., Pont D., Verdonschot P.F.M. & Friberg N. (2011) From natural to degraded rivers and back again: a test of restoration ecology theory and practice. Advances in Ecological Research 44, 119-209.

Feld C.K. (2012) Response of three lotic assemblages to riparian and catchment-scale land use: implications for designing catchment monitoring programmes. Freshwater Biology 58(4), 715-729.

Feld C.K., de Bello F. & Dolédec S. (2014) Biodiversity of traits and species both show weak responses to hydromorphological alteration in lowland river macroinvertebrates. Freshwater Biology 15(2), 233-248.

Ferrier S. (2002) Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Systematic Biology 51(2), 331-363.

Fielding A.H. & Bell J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38-49.

Filipe A.F., Lawrence J.E. & Bonada N. (2013) Vulnerability of stream biota to climate change in mediterranean climate regions: A synthesis of ecological responses and conservation challenges. Hydrobiologia 719(1), 331-351.

Franklin J., McCullough P. & Gray C. (2000) Terrain variables used for predictive mapping of vegetation communities in southern California. In: Wilson, J.P., Gallant, J.C. (ed.): Terrain Analysis: principles and applications. John Wiley & Sons.

Franklin J. (2009) Mapping species distributions: spatial inference and prediction. Cambridge University Press, 320pp.

Franklin J., Wejnert K.E., Hathaway S.A., Rochester C.J. & Fisher R.N. (2009) Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. Diversity and Distributions 15, 167-177.

Franklin J. (2010) Moving beyond static species distribution models in support of conservation biogeography. Diversity and Distributions 16(3), 321-330.

Free G., Solimini A.G., Rossaro B., Marziali L., Giacchini R., Paracchini B., Ghiani M., Vaccaro S. , Gawlik B.M., Fresner R., Santner G., Schönhuber M. & Cardoso A.C. (2009) Modelling lake macroinvertebrate species in the shallow sublittoral: Relative roles of habitat, lake morphology, aquatic chemistry and sediment composition. Hydrobiologia 633(1), 123-136.

Freeman E.A. & Moisen G. (2008) PresenceAbsence: An R Package for Presence-Absence Model Analysis. Journal of Statistical Software 23, 1-31. <http://www.jstatsoft.org/v23/i11>

Freeman E. (2007) PresenceAbsence: An R Package for Presence-Absence Model Evaluation. USDA Forest Service, Rocky Mountain Research Station, 507 25th street, Ogden, UT, USA.

Freeman M.C., Bowen Z.H. & Crance J.H. (1997) Transferability of habitat suitability criteria for fishes in warmwater streams. North American Journal of Fisheries Management 17, 20-31.

Friberg N., Sandin L., & Pedersen M.L. (2009) Assessing the effects of hydromorphological degradation on macroinvertebrate indicators in rivers: examples, constraints, and outlook. Integrated environmental assessment and management 5(1), 86-96.

Friedrich G. (1990). Eine Revision des Saprobiensystems. Zeitschrift für Wasser- und Abwasser-Forschung 23(4), 141-152.

Friedrich G. & Herbst V. (2004) Eine erneute Revision des Saprobiensystems - weshalb und wozu? Acta hydrochimica et hydrobiologica 32(1), 61-74.

Fukuda S., Tanakura T., Hiramatsu K., Harada M. (2014) Assessment of spatial habitat heterogeneity by coupling data-driven habitat suitability models with a 2D hydrodynamic model in small-scale streams. Ecological Informatics, in press.

Giordani P. & Incerti G. (2008) The influence of climate on the distribution of lichens: A case study in a borderline area (Liguria, NW Italy). Plant Ecology 195(2), 257-272.

Glozier N.E., Culp J.M. & Scrimgeour G.J. (1997) Transferability of habitat suitability curves for a benthic minnow, Rhinichthys cataractae. Journal of Freshwater Ecology 12, 379-393.

Graf W., Grasser U. & Weinzierl A. (2002a) Trichoptera. In: Moog, O. (ed.): Fauna Aquatica Austriaca, Lieferung 2002. Wasserwirtschafts-kataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Graf W., Grasser U. & Weinzierl A. (2002b) Plecoptera. In: Moog O. (ed.), Fauna Aquatica Austriaca, Lieferungen Edition 2002, Wasserwirtschaftskataster, Bundesministerium für Land und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Graf W., Lorenz A.W., Tierno de Figueroa J.M., Lücke S., López-Rodríguez M.J. & Davies C. (2009) Distribution and Ecological Preferences of European Freshwater Organisms. Volume 2 Plecoptera. Edited by Schmidt-Kloiber, A. & D. Hering. Pensoft Publishers (Sofia-Moscow). 262pp.

Graf, W., Murphy, J., Dahl, J., Zamora-Muñoz, C. & López-Rodríguez, M.J., 2008. Distribution and Ecological Preferences of European Freshwater Organisms. Volume 1 - Trichoptera. Edited by Schmidt-Kloiber, A. & D. Hering. Pensoft Publishers (Sofia-Moscow). 388pp.

Guisan A. & Zimmermann N.E. (2000) Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Guisan P. & Thuiller W. (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993-1009.

Haidekker A. & Hering D. (2007) Relationship between benthic insects (Ephemeroptera, Plecoptera, Coleoptera, Trichoptera) and temperature in small and medium-sized streams in Germany: A multivariate study. Aquatic Ecology 42(3), 463-481.

Hampe A. (2004) Bioclimate envelope models: what they detect and what they hide. Global Ecology and Biogeography 13, 469-471.

Hanley J.A. & McNeil B.J. (1982) The meaning and use of the area under a receiver operating characteristic (ROC) curve. Radiology 143, 29-36.

Harding J.S., Benfield E.F., Bolstad P.V., Helfman G.S. & Jones E.B.D. (1998) Stream biodiversity: the ghost of land use past. Proceedings of the national academy of sciences 95(25), 14843-14847.

Hastie T., Tibshirani R. & Friedman J.H. (2001) The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Springer, New York.

Haybach A. & Eiseler B. (2011) Rote Liste und Artenverzeichnis der Eintagsfliegen - Ephemeroptera - in Nordrhein-Westfalen 2. Fassung, Stand April 2011. [Red list and list of species of mayflies - Ephemeroptera from Northrhine-Westphalia], 553-563p. In: Rote Liste der gefaehrdeten Pflanzen, Pilze und Tiere in Nordrhein-Westfalen, 4. Fassung Band 2: Tiere 680p., LANUV NRW Recklinghausen .

Heidemann H. & Seidenbusch R. (2002) Die Libellenlarven Deutschlands. In: Die Tierwelt Deutschlands, 72. Teil, Goecke & Evers, Keltern.

Hering D., Buffagni A., Moog O., Sandin L., Sommerhäuser M., Stubauer I., Sandin L., Sommerhäuser M., Stubauer I., Feld C., Johnson R., Pinto P., Skoulikidis N., Verdonschot P. & Zahrádková S. (2003) The development of a system to assess the ecological quality

of streams based on macroinvertebrates–design of the sampling programme within the AQEM project. International Review of Hydrobiology 88, 345-361.

Hering D., Moog O., Sandin L. & Verdonschot P.F. (2004) Overview and application of the AQEM assessment system. Hydrobiologia 516(1-3), 1-20.

Hering D., Borja A., Carstensen J., Carvalho L., Elliott M., Feld C.K., Heiskanen A.-S., Johnson R.K., Moe J., Pont D., Solheim A.L. & Van de Bound W. (2010) The European Water Framework Directive at the age of 10: A critical review of the achievements with recommendations for the future. Science of the Total Environment 408, 4007-4019.

Hershkovitz Y., Dahm V. & Lorenz A.W. (2015) A multi-trait approach for the identification and protection of European freshwater species that are potentially vulnerable to the impacts of climate change. Ecological Indicators 50, 150-160.

Hill M. & Smith A. (1976) Principal Component Analysis of Taxonomic Data with Multi-State Discrete Characters. Taxon 25, 249-255.

Hirzel A.H., Le Lay G., Helfer V., Randin C. & Guisan A. (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecological Modelling 199, 142-152.

Hirzel A.H., & Le Lay G. (2008) Habitat suitability modelling and niche theory. Journal of Applied Ecology 45(5), 1372-1381.

Holm A. (1989) Ökologischer Bewertungsrahmen Fließgewässer (Bäche) für die Naturräume der Geest und des Östlichen Hügellandes in Schleswig-Holstein. Kiel: Landesamt für Naturschutz und Landschaftspflege des Landes Schleswig-Holstein. In: Schmedtje U. & Colling M. (1996) Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4/96.

Hosmer D.W. & Lemeshow S. (2000) Applied Logistic Regression. New York, Wiley-Interscience Publication, 392 pp. ISBN 0-471-61553-6.

Hutchinson G.E. (1957) Population Studies - Animal Ecology and Demography – Concluding Remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22, 415-427.

Hynes H.B.N. (1970) The Ecology of Running Waters. Liverpool University Press, Liverpool, UK.

Hynes H.B.N. (1975) The stream and its valley. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 19, 1-15.

IBM Corp. Released (2011) IBM SPSS Statistics for Windows, Version 20.0. Armonk, NY: IBM Corp.

Jähnig S.C., Lorenz A.W. & Hering D. (2009) Restoration effort, habitat mosaics, and macroinvertebrates - does channel form determine community composition? Aquatic Conservation: Marine and Freshwater Ecosystems 19(2), 157-169.

Jähnig S.C., Brabec K., Buffagni A., Erba S., Lorenz A.W., Ofenböck T., Verdonschot P.F.M. & Hering D. (2010) A comparative analysis of restoration measures and their effects on hydromorphology and benthic invertebrates in 26 central and southern European rivers. Journal of Applied Ecology 47, 671-680.

Jähnig S., Kuemmerlen M., Kiesel J., Domisch S., Cai Q., Schmalz B. & Fohrer N. (2012) Modelling of riverine ecosystems by integrating models: conceptual approach, a case study and research agenda. Journal of Biogeography 39, 2253-2263.

Janecek B.F.U., Moog O. & Waringer J. (1995) Odonata. In: Moog, O. (Ed.): Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

Januschke K. (2014) Morphological effects on colonization and succession of aquatic and riparian organism groups. PhD thesis, 113pp.

Jiménez-Valverde A. & Lobo J.M. (2006) The ghost of unbalanced species distribution data in geographical model predictions. Diversity and Distributions 12, 521-525.

Jiménez-Valverde A., Lobo J.M. & Hortal J. (2009) The effect of prevalence and its interaction with sample size on the reliability of species distribution models. Community Ecology 10(2), 196-205.

Jiménez-Valverde A., Lobo J.M., & Hortal J. (2008) Not as good as they seem: the importance of concepts in species distribution modelling. Diversity and Distributions 14(6), 885-890.

Jiménez-Valverde A. (2012) Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. Global Ecology and Biogeography 21, 498-507.

Jyväsjärvi J., Aroviita J. & Hämäläinen H. (2011) Evaluation of approaches for measuring taxonomic completeness of lake profundal macroinvertebrate assemblages. Freshwater Biology 56(9), 1876-1892.

Kail J. & Hering D. (2005) Using Large Wood to Restore Streams in Central Europe: Potential use and Likely Effects. Landscape Ecology 20, 755-772.

Kail J. & Hering D. (2009) The influence of adjacent stream reaches on the local ecological status of Central European mountain streams. River Research and Applications 25(5), 537-550.

Kearney M. (2006) Habitat, environment and niche: what are we modelling? Oikos 115, 186-191.

Kemp J.L., D.M. Harper & Crosa G.A. (1999) Use of 'functional habitats' to link ecology with morphology ad hydrology in river rehabilitation. Aquatic Conservation: Marine and Freshwater Ecosystems 9, 159-178.

Kiesel J., Hering D., Schmalz B. & Fohrer N. (2009) A transdisciplinary approach for modelling macroinvertebrate habitats in lowland streams. IAHS-AISH publication, 24-33.

Kis B. (1974) Plecoptera, Insecta. Fauna Republicii Socialiste Romania. Editura Academiei R.S.R., Bucuresti 8, 271pp.

Kleinwächter M. & Rickfelder T. (2007) Habitat models for a riparian carabid beetle: Their validity and applicability in the evaluation of river bank management. Biodiversity and Conservation 16(11), 3067-3081.

Kohavi R. (1995) A study of cross-validation and bootstrap for accuracy estimation and model selection. Proceedings of the Fourteenth International Joint Conference on Artificial Intelligence 2, 1137-1143.

Kohl R. (1994) Untersuchungen zur Ökologie der Köcherfliegen-Larven in Gewässern des Saarlandes. Lauterbornia 16, 51-67.

Kolkwitz R. & Marson M. (1909) Ökologie der tierischen Saprobien. Internationale Revue der gesamten Hydrobiologie 2, 126-152.

Kopp D., Figuerola J., Compin A., Santoul F. & Céréghino R. (2012) Local extinction and colonisation in native and exotic fish in relation to changes in land use. Marine and Freshwater Research 63(2), 175-179.

Kornis M.S. & van der Zanden M.J. (2010) Forecasting the distribution of the invasive round goby (*Neogobius melanostomus*) in Wisconsin tributaries to Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 67(3), 553-562.

Kraemer H.C. (1988) Assessment of 2 x 2 associations: Generalisation of signal detection methodology. The American Statistician 42, 37-49.

Kristensen E.A., Baattrup-Pedersen A. & Andersen H.E. (2012) Prediction of stream fish assemblages from land use characteristics: Implications for cost-effective design of monitoring programmes. Environmental Monitoring and Assessment 184(3), 1435-1448.

Kuemmerlen M., Domisch S., Schmalz B., Cai Q., Fohrer N. & Jähnig S.C. (2012) Integrierte Modellierung von aquatischen Ökosystemen in China: Arealbestimmung von Makrozoobenthos auf Einzugsgebietsebene. Hydrologie und Wasserbewirtschaftung 56, 185-192.

Kuemmerlen M., Schmalz B., Gusec B., Cai Q., Fohrer N. & Jähnig S.C. (2014) Integrating catchment properties in small scale species distribution models of stream macroinvertebrates. Ecological Modelling 277, 77-86.

Kusch J. (2015) Interacting influences of climate factors and land cover types on the distribution of caddisflies (Trichoptera) in streams of a central European low mountain range. Insect Conservation and Diversity 8, 92-101.

Lamberti G.A. & Resh V.H. (1979) Substrate relationships, spatial-distribution patterns, and sampling variability in a stream caddisfly population. Environ Entomol 8, 561-567.

Lamouroux N., Mérigoux S., Dolédec S. & Snelder T.H. (2013) Transferability of hydraulic preference models for aquatic macroinvertebrates. River Research and Applications 29, 933-937.

[LANUV 2011] Landesamt für Umwelt Natur und Verbraucherschutz NRW (2011) Rote Liste der gefährdeten Pflanzen, Pilze und Tiere in Nordrhein-Westfalen, 4. Fassung 2011. Band 2: Tiere. Recklinghausen: LANUV Fachbericht 36.

[LAWA 2000] Länderarbeitsgemeinschaft Wasser (2000) Gewässerstrukturgütekartierung in der Bundesrepublik Deutschland: Verfahren für kleine und mittelgroße Fließgewässer. Kulturbuch-Verlag, 166 pp.

Lawrence J.E., Lunde K.B., Mazor R.D., Beche L.A., McElravy E.P. & Resh V.H. (2010) Long-term macroinvertebrate responses to climate change: implications for biological assessment in mediterranean-climate streams. Journal of the North American Benthological Society 29(4), 1424-1440.

Lawson C.R., Hodgson J.A., Wilson R.J. & Richards S.A. (2014) Prevalence, thresholds and the performance of presence-absence models. Methods in Ecology and Evolution 5, 54-64.

Le Roux P.C., Lenoir J., Pellissier L., Wisz M.S. & Luoto M. (2013) Horizontal, but not vertical, biotic interactions affect fine-scale plant distribution patterns in a low-energy system. Ecology 94, 671-682.

Le Roux P.C., Pellissier L., Wisz M.S. & Luoto M. (2014) Incorporating dominant species as proxies for biotic interactions strengthens plant community models. Journal of Ecology 102(3), 767-775.

Leathwick J.R, Elith J. & Hastie T. (2006) Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. Ecological Modelling 199, 188-196.

Lepori F., Palm D., Brännäs E. & Malmqvist B. (2005) Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? Ecological Applications 15, 2060-2071.

Liang L., Fei S., Ripy J.B., Blandford B.L. & Grossardt T. (2012) Stream habitat modelling for conserving a threatened headwater fish in the upper Cumberland River, Kentucky. River Research and Applications 29(10), 1207-1214.

Linke S., Norris R.H. & Pressey R.L. (2008) Irreplaceability of river networks towards catchment-based conservation planning. Journal of Applied Ecology 45(5), 1486-1495.

Liu C., Berry P.M., Dawson T.P. & Pearson R.G. (2005) Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28, 385-393.

Lobo J.M., Jiménez-Valverde A. & Real R. (2008) AUC: a misleading measure of the performance of predictive distribution models. Global Ecology and Biogeography 17, 145-151.

Lobo J.M., Jiménez-Valverde A. & Hortal J. (2010) The uncertain nature of absences and their importance in species distribution modelling. Ecography 33(1), 103-114.

Lock K. & Goethals P.L.M. (2013) Habitat suitability modelling for mayflies (Ephemeroptera) in Flanders (Belgium). Ecological Informatics 17, 30-35.

Lock K. & Goethals P.L.M. (2014) Predicting the occurrence of stoneflies (Plecoptera) on the basis of water characteristics, river morphology and land use. Journal of Hydroinformatics 16, 812-820.

Lohse K.A., Newburn D.A., Opperman J.J., & Merenlender A.M. (2008) Forecasting relative impacts of land use on anadromous fish habitat to guide conservation planning. Ecological Applications 18(2), 467-482.

Lorenz A.W., Hering D., Feld C.K. & Rolauffs P. (2004) A new method for assessing the impact of hydromorphological degradation on the macroinvertebrate fauna of five German stream types. Hydrobiologia 516, 107-127.

Lorenz A.W., Jähnig S.C. & Hering D. (2009) Re-Meandering German lowland streams: qualitative and quantitative effects of restoration measures on hydromorphology and macroinvertebrates. Environmental Management 44, 745-754.

Lorenz A.W. & Feld C.K. (2013) Upstream river morphology and riparian land use overrule local restoration effects on ecological status assessment. Hydrobiologia 704(1), 489-501.

[LUA & MUNLV 2005] Landesumweltamt Nordrhein-Westfalen (LUA) & Ministerium für Umwelt und Naturschutz, Landwirtschaft und Verbraucherschutz des Landes Nordrhein-Westfalen (2005) Gewässerstrukturgüte in Nordrhein-Westfalen – Bericht 2005, 109pp.

[LUA 1998] Landesumweltamt Nordrhein-Westfalen (1998) Merkblätter Nr. 14 Gewässerstrukturgüte in Nordrhein-Westfalen – Kartieranleitung, 1. Auflage.

Luck G.W. (2002) The habitat requirements of the rufous treecreeper (*Climacteris rufa*). 2. Validating predictive habitat models. Biological Conservation 105, 395-403.

Luoto M., Pöyry J., Heikkinen R.K. & Saarinen K. (2005) Uncertainty of bioclimate envelope models based on the geographical distribution of species. Global Ecology and Biogeography 14(6), 575-584.

Luoto T.P. (2011) The relationship between water quality and chironomid distribution in Finland - A new assemblage-based tool for assessments of long-term nutrient dynamics. Ecological Indicators 11(2), 255-262.

Maibach A. & Meier C. (1987) Verbreitungsatlas der Libellen der Schweiz (Odonata, mit roter Liste). Documenta Faunistica Helvetiae 4. Neuchâtel. In: Schmedtje, U. & Colling, M. (1996): Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4/96.

Malicky H. (2004) Atlas of European Trichoptera. Second Edition. Springer Verlag, 359pp.

Malmqvist B. (2002) Aquatic invertebrates in riverine landscapes. Freshwater Biology 47, 679-694.

Manel S., Dias J.M., Buckton S.T. & Ormerod S.J. (1999a) Alternative methods for predicting species distribution: an illustration with Himalayan river birds. Journal of Applied Ecology 36, 734-747.

Manel S., Dias J.M. & Ormerod S. (1999b) Comparing discriminant analysis, neural networks and logistic regression for predicting species distributions: a case study with a Himalayan river bird. Ecological Modelling 120, 337-347.

Manel S., Williams H. & Ormerod S.J. (2001) Evaluating presence-absence models in ecology: the need to account for prevalence. Journal of Applied Ecology 38(5), 921-931.

McAlpine C.A., Rhodes J.R., Bowen M.E., Lunney D., Callaghan J.G., Mitchell D.L. & Possigham H.P. (2008) Can multiscale models of species' distribution be generalized from region to region? A case study of the koala. Journal of Applied Ecology 45, 549-557.

McCune B. (2006) Non-parametric habitat models with automatic interactions. Journal of Vegetation Science 17, 819-830.

McCune B. (2007) Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. Journal of Vegetation Science 18, 751-754.

McCune B. (2009) Nonparametric Multiplicative Regression for Habitat Modeling. <http://www.pcord.com/NPMRintro.pdf>.

McCune B. & Mefford M.J. (2009) HyperNiche. Nonparametric Multiplicative Habitat Modeling, Version 2.20. MjM Software, Gleneden Beach, Oregon, U.S.A.

McPherson J.M., Jetz W. & Rogers D.J. (2004) The effects of species' range sizes on the accuracy of distribution models: ecological phenomenon or statistical artefact? Journal of Applied Ecology 41, 811-823.

McPherson J.M. & Jetz W. (2007) Effects of species' ecology on the accuracy of distribution models. Ecography 30, 153-151.

Meier C., Böhmer J., Biss R., Feld C., Haase P., Lorenz A., Rawer-Jost C., Rolauffs P., Schindehütte K., Schöll F., Sundermann A., Zenker A. & Hering D. (2006) Weiterentwicklung und Anpassung des nationalen Bewertungssystems für Makrozoobenthos an neue internationale Vorgaben. Abschlussbericht im Auftrag des Umweltbundesamtes. http://www.fliessgewaesserbewertung.de [Juni 2006].

Miller J.R., Turner M.G., Smithwick E.A.H., Dent C.L. & Stanley E.H. (2004) Spatial extrapolation: the science of predicting ecological patterns and processes. Bioscience 54, 310-320.

Miller J.A. (2012) Species distribution models: Spatial autocorrelation and non-stationarity. Progress in Physical Geography 36, 681-692.

Minshall G.W. (1988) Stream ecosystem theory – a global perspective. Journal of the North American Benthological Society 7, 263-288.

Miserendino M.L., Casaux R., Archangelsky M., Di Prinzio C.Y., Brand C., & Kutschker A.M. (2011) Assessing land-use effects on water quality, in-stream habitat, riparian ecosystems and biodiversity in Patagonian northwest streams. Science of the Total Environment 409(3), 612-624.

Mladenoff D.J., Sickley T.A. & Wydeven A. (1999) Predicting gray wolf landscape recolonization: logistic regression models vs. new field data. Ecological Applications 9, 37-44.

Moilanen A., Leathwick J. & Elith J. (2008) A method for spatial freshwater conservation prioritization. Freshwater Biology 53(3), 577-592.

Mouton A.M., De Bates B. & Goethals P.L.M. (2010) Ecological relevance of performance criteria for species distribution models. Ecological Modelling 221, 1995-2002.

[MUNLV 2005] Ministerium für Umwelt und Naturschutz, Landwirtschaft und Verbraucherschutz des Landes Nordrhein-Westfalen (2005) Ergebnisbericht Ruhr, Wasserrahmenrichtlinie in NRW – Bestandsaufnahme, 445pp.

Murray J.V., Low Choy S., McAlpine C.A., Possigham H.P. & Goldizen A.W. (2011) Evaluating model transferability for a threatened species to adjacent areas: Implications for rock-wallaby conservation. Austral Ecology 36, 76-89.

Nagelkerke N.J.D. (1992) Maximum Likelihood Estimation of Functional Relationships, Pays-Bas. Lecture Notes in Statistics 69. ISBN 0-387-97721-X.

Naimi B. (2013) usdm: Uncertainty analysis for species distribution models. R package version 1.1-12. <http://CRAN.R-project.org/package=usdm>

Neilson R.P., King G.A., & Koerper G. (1992) Toward a rule-based biome model. Landscape Ecology 7(1), 27-43.

Neu P.J. (Stand 2011) Trichoptera-RP - die Köcherfliegenseiten von P.J. Neu. Informationen zu Ökologie, Taxonomie und Verbreitung der Köcherfliegen in Deutschland. <http://www.trichoptera-rp.de/html/taxonomie.html>

Neu P.J. & Tobias W. (2004) Die Bestimmung der in Deutschland vorkommenden Hydropsychidae (Insecta: Trichoptera). Lauterbornia 51, 68pp.

Olden J.D. & Jackson D.A. (2000) Torturing data for the sake of generality: how valid are our regression models? Ecoscience 7, 501-510.

Olden J.D. & Jackson D.A. (2002) A comparison of statistical approaches for modelling fish species distributions. Freshwater Biology 47, 1976-1995.

Olden J.D., Jackson D.A. & Peres-Neto P.R. (2002) Predictive models of fish species distributions: a note on proper validation and chance predictions. Transactions of the American Fisheries Society 131, 329-336.

Osborne P.E., Alonso J.C. & Bryant R.G. (2001) Modelling landscape-scale habitat use using GIS and remote sensing: a case study with great bustards. Journal of Applied Ecology 38, 458-471.

Osborne P.E. & Suárez-Seoane S. (2002) Should data be partitioned spatially before building large-scale distribution models? Ecological Modelling 157, 249-259.

Palmer M., Swan C., Nelson K., Silver P. & Alvestad R. (2000) Streambed landscapes: evidence that stream invertebrates respond to the type and spatial arrangement of patches. Landscape Ecology 15, 563-576.

Palmer M.A., Menninger H.L. & Bernhardt E. (2010) River restoration, habitat heterogeneity and biodiversity: a failure of theory or practice? Freshwater Biology 55, 205-222.

Pařil P., Bojková J., Špaček J. & Helešic J. (2008) Ecology of Leuctra geniculata (Plecoptera: Leuctridae), an Atlantomediterranean species on the north-eastern border of its area. Biologie 63(4), 574-581.

Park S.H., Goo J.M. & Jo C.-H. (2004) Receiver Operating Characteristic (ROC) Curve: Practical Review for Radiologists. Korean Journal of Radiology 5, 11-18.

Parkyn S.M. & Smith B.J. (2011) Dispersal constraints for stream invertebrates: setting realistic timescales for biodiversity restoration. Environmental management 48, 602-614.

Pearce J. & Ferrier S. (2000) Evaluating the predictive performance of habitat models developed using logistic regression. Ecological Modelling 133, 225-245.

Pearman P.B., Guisan A., Broennimann O. & Randin C.F. (2008) Niche dynamics in space and time. Trends in Ecology & Evolution 23, 149-58.

Pearson R.G. & Dawson T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12(5), 361-371.

Peterson A.T. (2001) Predicting Species' Geographic Distributions Based on Ecological Niche Modeling. The Condor 103, 599-605.

Peterson A.T., Ortega-Huerta M.A., Bartley J., Sanchez-Cordero V., Soberon J., Buddemeier R.W. & Stockwell D.R.B. (2002) Future projections for mexican faunas under global climate change scenarios. Nature 416, 626-629.

Peterson A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. The Quarterly Review of Biology 78, 419-433.

Peterson A.T., Papes M. & Eaton M. (2007) Transferability and model evaluation in ecological niche modeling: a comparison of GARP and Maxent. Ecography 30, 550-560.

Phillips S.J. (2008) Transferability, sample selection bias and background data in presence-only modeling: a response to Peterson et al. (2007). Ecography 31, 272-278.

Pitsch T. (1993) Zur Larvaltaxonomie, Faunistik und Ökologie mitteleuropäischer Fließwasser-Köcherfliegen (Insecta: Trichoptera). Landschaftsentwicklung und Umweltforschung - Schriftenreihe des Fachbereichs Landschaftsentwicklung der Technischen Universität Berlin. Sonderheft S8, 316pp.

Poff N.L. (1997) Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology. Journal of the North American Benthological Society 16, 391-409.

Ponader K.C. & Potapova M.G. (2007) Diatoms from the genus Achnanthidium in flowing waters of the Appalachian Mountains (North America): Ecology, distribution and taxonomic notes. Limnologica 37(3), 227-241.

Pottgiesser,T. & Sommerhäuser M. (2008) Beschreibung und Bewertung der deutschen Fliessgewässertypen. Steckbriefe und Anhang. Download über www.fliessgewässerbewertung.de

Power M. (1993) The predictive validation of ecological and environmental models. Ecological Modelling 68, 33-50.

Prié V., Molina Q., & Gamboa B. (2014) French naiad (Bivalvia: Margaritiferidae, Unionidae) species distribution models: prediction maps as tools for conservation. Hydrobiologia 735(1), 81‑94.

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>

R Development Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>

Randin C.F., Dirnbock T., Dullinger S., Zimmermann N.E., Zappa M. & Guisan A. (2006) Are niche-based species distribution models transferable in space? Journal of Biogeography 33, 1689-1703.

Raven P.J., Homes N.T.H., Charrier P., Dawson F.H., Naura M. & Boon P.J. (2002) Towards a harmonized approach for hydromorphological assessment of rivers in Europe: a qualitative comparison of three survey methods. Aquatic Conservation: Marine and Freshwater Ecosystems 12, 405-424.

Reusser D.A. & Lee II H. (2008) Predictions for an invaded world: a strategy to predict the distribution of native and non-indigenous species at multiple scales. ICES Journal of Marine Science 65, 742-745.

Richardson D.M. & Whittaker R.J. (2010) Conservation biogeography – foundations, concepts and challenges. Diversity and Distributions 16, 313-320.

Robertson E.A. & Zweig M.H. (1981) Use of receiver operating curves to evaluate the clinical performance of analytical systems. Clinical Chemistry 27, 1569-1574.

Robertson E.A., Zweig M.H. & Van Steirteghem M.D. (1983) Evaluating the clinical accuracy of laboratory tests. American Journal of Clinical Pathology 79, 78-86.

Robin X., Turck N., Hainard A., Tiberti N., Lisacek F., Sanchez J.-C. & Müller M. (2011) pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinformatics 12, 77p. <http://www.biomedcentral.com/1471-2105/12/77/>

Rolauffs P. (2006) Modellierung ökologischer Zusammenhänge bei Mittelgebirgsbächen unter Berücksichtigung von Gewässermorphologie und Landnutzung im Hinblick auf die biozönotische Bewertung mittels Makroinvertebraten. Hochschulschrift der Universität Duisburg-Essen, Dissertation.

Roni P., Bennett T., Morley S., Pess G.R., Hanson K., Van Slyke D. & Olmstead P. (2006) Rehabilitation of bedrock stream channels: the effects of boulder weir placement on aquatic habitat and biota. River Research and Applications 22, 967-980.

Ruhrverband (2009) – Ruhrgütebericht 2008, 197pp.

Ruhrverband (2013) – Ruhrgütebericht 2012, 209pp.

Rykiel E.J. (1996) Testing ecological models: the meaning of validation. Ecological Modelling 90, 229-244.

Sánchez-Ortega A., Alba-Tercedor J. & Tierno de Figueroa J.M. (2002) Lista faunística y bibliográfica de los Plecópteros de la Península Ibérica e Islas Baleares. Publicaciones de la Asocíacion española de Limnología Nr.16.

Sauer F. (1988) Wasserinsekten. Fauna-Verlag Krefeld, 161pp.

Scherr M.A., Wooster D. & Rao S. (2011) Interactions between macroinvertebarte taxa and complex environmental gradients influencing abundance and distribution in the Umatilla River, Northeastern Oregon. Journal of Freshwater Ecology 26(2), 255-266.

Schmedtje U. & Kohmann F. (1992) Bestimmungsschlüssel für Saprobier-DIN-Arten (Makroorganismen). München: Informationsberichte des Bayer. Landesamt für Wasserwirtschaft Heft 2/88.

Schmedtje U. & Colling M. (1996) Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4/96.

Schmidt-Kloiber A. & Hering D. (eds.) (2012) www.freshwaterecology.info - the taxa and autecology database for freshwater organisms, version 5.0 (accessed on 30.10.2013).

Schorr M. (1990) Grundlagen zu einem Artenhilfsprogramm Libellen der Bundesrepublik Deutschland. Bilthoven: Ursus Scientific Publishers.

Schröder P. (1985) Hydropsychidae, Philopotamidae und Polycentropodidae (Trichoptera: Köcherfliegen) in den Fließgewässern um Freiburg im Breisgau. Mitteilungen des badischen Landesvereins für Naturkunde und Naturschutz e.V. Freiburg im Breisgau 13, 429-437.

Schroeder T.A., Hamann A., Wang T. & Coops N.C. (2010) Occurrence and dominance of six Pacific Northwest conifer species. Journal of Vegetation Science 21(3), 586-596.

Schuhmacher H. & Schremmer F. (1970) Die Trichopteren des Odenwaldbaches “Steinach” und ihr ökologischer Zeigerwert. Internationale Revue der gesamten Hydrobiologie 55(3), 335-358.

Segurado P. & Araújo M.B. (2004) An evaluation of methods for modeling species distributions. Journal of Biogeography 31, 1555-1568.

Shrestha G., Petersen S.L. & St. Clair L.L. (2012) Predicting the distribution of the air pollution sensitive lichen species Usnea hirta. The Lichenologist 44(4), 511-521.

Sing T., Sander O., Beerenwinkel N. & Lengauer T. (2009) ROCR: Visualizing the performance of scoring classifiers. R package version 1.0-4. <http://CRAN.R-Project.org/package=ROCR>

Sládeček V. (1965) The future of the saprobity system. Hydrobiologia 25, 518‑537.

Sondermann M., Gies M., Hering D., Schröder M. & Feld C.K. (2015) Modelling the effect of in-stream and terrestrial barriers on the dispersal of aquatic insect species: a case study from a Central European mountain catchment. Fundamental and Applied Limnology, in press.

Sponseller R.S., Benfield E.F. & Valett H.M. (2001) Relationships between land use, spatial scale, and stream macroinvertebrate communities. Freshwater Biology 46, 1409-1424.

Statzner B., Gore J.A. & Resh V.H. (1988) Hydraulic stream ecology: Observed patterns and potential applications. Journal of the North American Benthological Society 7, 307-360.

Statzner B., Hildrew A.G. & Resh V.H. (2001) Species traits and environmental constraints: entomological research and the history of ecological theory. Annual Review of Entomology 46, 291-316.

Statzner B. & Dolédec S. (2011) Phylogenetic, Spatial, and Species-Trait Patterns across Environmental Gradients: the Case of Hydropsyche (Trichoptera) along the Loire River. International Review of Hydrobiology 96(2), 121-140.

Sternberg K., & Buchwald R. (1999) Die Libellen Baden-Württembergs. Band 1: Allgemeiner Teil, Kleinlibellen (Zygoptera). Verlag Eugen Ulmer.

Stewart K.W. & Stark B.P. (1993) Nymphs of North American Stonefly Genera (Plecoptera). University of North Texas Press, Denton, Texas.

Stoks R. & Córdoba-Aguilar A. (2012) Evolutionary ecology of Odonata: a complex life cycle perspective. Annual Review of Entomology 57, 249-265.

Stockwell D.R.B. & Peterson A.T. (2002) Effects of sample size on accuracy of species distribution models. Ecological Modelling 148, 1-13.

Stockwell D. (2006) Niche Modeling: Predictions from Statistical Distributions. Boca Raton, FL: Chapman and Hall/CRC.

Stoll S., Sundermann A., Lorenz A.W., Kail J. & Haase P. (2013) Small and impoverished regional species pools constrain colonisation of restored river reaches by fishes. Freshwater Biology 58, 664-674.

Studemann D., Landolt P., Sartori M., Hefti D. & Tomka I. (1992) Insecta Helvetica. Fauna. 9. Ephemeroptera. Hrsg. Schweizerische Entomologische Gesellschaft, Redakteur: Sauter.

Sundblad G., Härma M., Lappalainen A., Urho L. & Bergström U. (2009) Transferability of predictive fish distribution models in two coastal systems. Estuarine, Coastal and Shelf Science 83, 90-96.

Sundermann A., Antons C., Cron N., Lorenz A.W., Hering D. & Haase P. (2011a) Hydromorphological restoration of running waters: effects on benthic invertebrate assemblages. Freshwater Biology 56, 1689-1702.

Sundermann A., Stoll S. & Haase P. (2011b) River restoration success depends on the species pool of the immediate surroundings. Ecological Applications 21, 1962-1971.

Sundermann A., Gerhardt M., Kappes H. & Haase P. (2013) Stressor prioritisation in riverine ecosystems: Which environmental factors shape benthic invertebrate assemblage metrics? Ecological Indicators 27, 83-96.

Swets K.A. (1988) Measuring the accuracy of diagnostic systems. Science 240, 1285-1293.

Tang H., Song M.-Y., Cho W.-S., Park Y.-S. & Chon T.-S. (2010) Species abundance distribution of benthic chironomids and other macroinvertebrates across different levels of pollution in streams. Annales de Limnologie 46(1), 53-66.

Theinemann A. (1954) Ein drittes biozonotisches Grundprinzip. Archiv für Hydrobiologie 49, 421-422.

Thomas J.A. & Bovee K.D. (1993) Application and testing of a procedure to evaluate transferability of habitat suitability criteria. Regulated Rivers: Research and Management 8, 288-294.

Thomas C.D., Cameron A., Green R.E., Bakkenes M., Beaumont L.J., Collingham Y.C., Erasmus B.F.N., de Siqueira M.F., Grainger A., Hannah L., Hughes L., Huntley B., van Jaarsveld A.S., Midgley G.F., Miles L., Ortega-Huerta M.A., Peterson A.T., Phillips O.L. & Williams S.E. (2004) Extinction risk from climate change. Nature 427(6970), 145-148.

Thuiller W., Richardson D.M., Pyšek P., Midgley G.F., Hughes G.O. & Rouget M. (2005b) Niche-based modelling as a tool for predicting the risk of alien plant invasions at a global scale. Global Change Biology 11, 2234-2250.

Thuiller, W., 2003. BIOMOD - Optimizing predictions of species distributions and projecting potential future shifts under global change. Global Change Biology 9, 1353-1362.

Thuiller W., Lavorel S. & Araújo M.B. (2005a) Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecology and Biogeography 14, 347-357.

Thuiller W., Richardson D.M., Pysek P., Midgley G.F., Hughes G.O. & Rouget M. (2005b) Niche-based modeling as a tool for predicting the global risk of alien plant invasions. Global Change Biology 11, 2234-2250.

Tobias W. & Tobias D. (1981) Trichoptra Germanica - Bestimmungstafeln für die deutschen Köcherfliegen Teil I Imagines. Courier Forschungsinstitut Senckenberg 49, Frankfurt a.M., 671pp.

Tockner K. & Ward J.V. (1999) Biodiversity along riparian corridors. Archiv für Hydrobiologie 115, 293-310.

Tognelli M.F., Silva-García C., Labra F.A. & Marquet P.A. (2005) Priority areas for the conservation of coastal marine vertebrates in Chile. Biological Conservation 126(3), 420-428.

Townsend C.R. & Hildrew A.G. (1994) Species traits in relation to a habitat templet for river systems. Freshwater Biology 31, 265-275.

Tsoar A., Allouche O., Steinitz O., Rotem D. & Kadmon R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distributions 13, 397-405.

Tsoar A., Allouche O., Steinitz O., Rotem D. & Kadmon R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. Diversity and Distributions 13, 397-405.

Tuanmu M.-N., Viña A., Roloff G.J., Liu W., Ouyang Z., Zhang H. & Liu J. (2011) Temporal transferability of wildlife habitat models: implications for habitat monitoring. Journal of Biogeography 38, 1510-1523.

Valladolid M., Martínez-Bastida J.J. & Arauzo M. (2007) Los Hydropsychidae (Insecta: Trichoptera) del río Oja (La Rioja, España). Limnetica 26(1), 199-208.

Van Steirteghem A.C., Zweig M.H., Robertson E.A., Bernard R.M., Putzeys G.A. & Bieva C. (1982) Comparison of the effectiveness of four clinical chemical assays in classifying patients' chest pain. Clinical Chemistry 28, 1319-1324.

Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 31, 130-137.

Vanreusel W., Maes D. & Van Dyck H. (2007) Transferability of species distribution models: a functional habitat approach for two regionally threatened butterflies. Conservation Biology 21, 201-212.

Vaughan I.P. & Ormerod S.J. (2005) The continuing challenges of testing species distribution models. Journal of Applied Ecology 42, 720-730.

Vaughan I.P., Diamond M., Gurnell A.M., Hall K.A., Jenkins A., Milner N.J., Naylor L.A., Sear D.A., Woodward G. & Ormerod S.J. (2009) Integrating ecology with hydromorphology: a priority for river science and management. Aquatic Conservation: Marine and Freshwater Ecosystems 19, 113-125.

Vinson M.R. & Hawkins C.P. (1998) Biodiversity of stream insects: variation at local, basin and regional scales. Annual Review of Entomology 43, 271-293.

Ward J.V. & Stanford J.A. (1979) Ecological factors controlling stream zoobenthos with emphasis on thermal modification of regulated streams. In Ward, J. V. & J. A. Stanford (eds), The Ecology of Regulated Streams. Plenum, New York, 35-55.

Ward J.V. (1989) The Four-Dimensional Nature of Lotic Ecosystems. Journal of the North American Benthological Society, 2-8.

Ward J.V. & Tockner K. (2001) Biodiversity: towards a unifying theme for river ecology. Freshwater Biology 46, 807-819.

Ward J.V., Tocker K., Arscott D.B. & Claret C. (2002) Riverine landscape diversity. Freshwater Biology 47, 517-539.

Waringer J. & Graf W. (1997) Atlas der österreichischen Köcherfliegenlarven unter Einschluß der angrenzenden Gebiete. Facultas-Universitätsverlag: 286p. + Ergänzungen und Berichtigungen zum Atlas der österreichischen Köcherfliegenlarven unter Einschluß der angrenzenden Gebiete (2004). Fakultas-Universitätsverlag, 28pp.

Wasson J.G., Villeneuve B., Iital A., Murray-Bligh J.O.H.N., Dobiasova M., Bacikova S., Timm, H., Pella H., Mengin N. & Chandesris A. (2010) Large-scale relationships between basin and riparian land cover and the ecological status of European rivers. Freshwater Biology 55(7), 1465-1482.

Welton J.S. (1979) Life-history and production of the amphipod *Gammarus pulex* in a Dorset chalk stream. Freshwater Biology 9(3), 263-275.

Wenger S.J. & Olden J.D. (2012) Assessing transferability of ecological models: an underappreciated aspect of statistical validation. Methods in Ecology and Evolution 3, 260-267.

Westhoff J.T., Rabeni C.F. & Sowa S.P. (2011) The distributions of one invasive and two native crayfishes in relation to coarse-scale natural and anthropogenic factors. Freshwater Biology 56(12), 2415-2431.

Wiens J.A. (2002) Riverine landscapes: taking landscape ecology into the water. Freshwater Biology 47, 501-515.

Wilson C.D., Roberts D., & Reid N. (2011) Applying species distribution modelling to identify areas of high conservation value for endangered species: A case study using *Margaritifera margaritifera* (L.). Biological Conservation 144(2), 821-829.

Woodward G. & Hildrew A. (2002) Food web structure in riverine landscapes. Freshwater Biology 47, 777-798.

Woolf A., Nielsen C.K., Weber T. & Gibbs-Kieninger T.J. (2002) Statewide modeling of bobcat, *Lynx rufus*, habitat in Illinois, USA. Biological Conservation 104, 191-198.

Yost A.C. (2008) Probabilistic modeling and mapping of plant indicator species in a Northeast Oregon industrial forest, USA. Ecological Indicators 8(1), 46-56.

Zanini F., Pellet J. & Schmidt B.R. (2009) The transferability of distribution models across regions: an amphibian case study. Diversity and Distributions 15, 469-480.

Zelinka M. & Marvan P. (1961) Zur Präzisierung der biologischen Klassifikation der Reinheit fließender Gewässer. Archiv für Hydrobiologie 57, 389-407.

Zharikov Y., Lank D.B. & Cooke F. (2007) Influence of landscape pattern on breeding distribution and success in a threatened Alcid, the marbled murrelet: model transferability and management implications. Journal of Applied Ecology 44, 748-759.

Zurell D., Jeltsch F., Dormann C.F. & Schröder B. (2009) Static species distribution models in dynamically changing systems: how good can predictions really be? Ecography 32, 733-744.

Zuur A., Ieno E.N. & Smith G.M. (2007) Analysing ecological data. Springer Science & Business Media.

Zweig M.H. & Campbell G. (1993) Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine. Clinical Chemistry 39, 561-577.

Zweig M.H., Broste S.K. & Reinhart R.A. (1992) ROC curve analysis: an example showing the relationships among serum lipid and apolipoprotein concentration in identifying patients with coronary artery disease. Clinical Chemistry 38, 1425-1428.

Zwick P. (1992) Stream habitat fragmentation – a threat to biodiversity. Biodiversity & Conservation 1, 733-744.

Zwick P. (2004) Key to the West Paleartic genera of stoneflies (Plecoptera) in the larval stage. Limnologica 34, 315-348.

Appendix

The Appendix is submitted as data files on a CD attached to this thesis.

Raw data collection:

Appendix 1a Field protocols

Appendix 1b Environmental data of 225 sampling sites

Appendix 1c Species presence/absence per 225 sampling sites

Appendix 1d Aggregation of physical habitat quality (aggregation, resolution, abbreviations)

Appendix 1e Aggregation of ATKIS land use categories

Appendix 1f Physical habitat quality assessment scores and land use percentages of all 100 m sections in the study area

Appendices to chapter 4:

Appendix 2a Gradients of broad-scale variables

Appendix 2b Gradients of fine-scale (local) variables

Appendix 2c Spearman rank correlation coefficients of the environmental variables

Appendix 2d Gradients of topographical variables after subsampling procedure

Appendix 2e Concordance of predictions within and between watersheds

Appendix 2f Results of SDMs including local predictors

Appendices to chapter 5:

Appendix 3a Predictors, sensitivity of predictors and significance of NPMR and LR models 2010

Appendix 3b Prediction maps of all model species

Appendix 3c Interrelation of cross-validated and field validated model and predictive performance measures (xR^2, AUC)

Appendix 3d Correlations between model and predictive performance measures (xR^2, AUC, PCC, TSS) and species prevalence

Appendix 3e Comparison of model prediction performance measures (false negative predictions [FN%] and false positive predictions [FP%]) against species prevalence

Appendix 3f Performance measures of field validation and independent validation

Curriculum vitae

Der Lebenslauf ist in der Online-Version aus Gründen des Datenschutzes nicht enthalten.

Eidesstattliche Erklärungen

Hiermit erkläre ich, gem. § 6 Abs. (2) f) der Promotionsordnung der Fakultäten für Biologie, Chemie und Mathematik zur Erlangung der Dr. rer. nat., dass ich das Arbeitsgebiet, dem das Thema „*Species distribution modelling of stream macroinvertebrates at the catchment scale*“ zuzuordnen ist, in Forschung und Lehre vertrete und den Antrag von Frau Maria Gies befürworte und die Betreuung auch im Falle eines Weggangs, wenn nicht wichtige Gründe dem entgegenstehen, weiterführen werde.

Essen, den _____ _____

Unterschrift eines Mitglieds der Universität Duisburg-Essen

Hiermit erkläre ich, gem. § 7 Abs. (2) c) + e) der Promotionsordnung Fakultäten für Biologie, Chemie und Mathematik zur Erlangung des Dr. rer. nat., dass ich die vorliegende Dissertation selbständig verfasst und mich keiner anderen als der angegebenen Hilfsmittel bedient habe.

Essen, den _____ _____

Unterschrift der Doktorandin

Hiermit erkläre ich, gem. § 7 Abs. (2) d) + f) der Promotionsordnung der Fakultäten für Biologie, Chemie und Mathematik zur Erlangung des Dr. rer. nat., dass ich keine anderen Promotionen bzw. Promotionsversuche in der Vergangenheit durchgeführt habe und dass diese Arbeit von keiner anderen Fakultät/Fachbereich abgelehnt worden ist.

Essen, den _____ _____

Unterschrift der Doktorandin